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A MONOGRAPH OF LYONIA (ERICACEAE)*

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TAXONOMIC TREATMENT

Lyonia Nutt. Gen. N. Am. Pl. 1: 266. 1818, *nomen cons.*, non *Lyonia* Ell. Sketch Bot. S. Carolina Georgia 1: 316. 1817 (= *Cynanchum* L., Asclepiadaceae), nec *Lyonia* Raf. Med. Repos. New York, ser. 2. 5: 353. 1803 (= *Polygonella* Michaux, Polygonaceae). *Xolisma* Raf. Am. Mon. Mag. Crit. Rev. 4: 193. 1819. LECTOTYPE SPECIES: *Lyonia ferruginea* (Walter) Nutt.; see I.C.B.N. 261. 1956, and Rickett & Stafleu, Taxon 9: 75. 1960.

Neopieris Britton in Britton & Br. Illus. Fl. ed. 2. 2: 690. 1913. TYPE SPECIES: *Neopieris mariana* (L.) Britton (= *Lyonia mariana* (L.) D. Don).

Desmothamnus Small, Shrubs Florida, 96. 1913. TYPE SPECIES: *Desmothamnus lucidus* (Lam.) Small (= *Lyonia lucida* (Lam.) K. Koch).

Arsenococcus Small in Small & Carter, Fl. Lancaster Co. 218. 1913. TYPE SPECIES: *Arsenococcus ligustrinus* (L.) Small (= *Lyonia ligustrina* (L.) DC.).

Evergreen or deciduous shrubs or trees, often from an underground, woody, globose to elongated burl, or occasionally forming thickets by means of horizontal underground rhizomes, with terete or angled branches and gray to reddish brown, longitudinally furrowed bark. Indumentum of unicellular hairs and multicellular, biseriate-stalked, ferruginous, peltate scales or swollen-headed hairs. Buds ovoid to nearly conical or flattened and triangular in outline, usually with 2 outer, imbricate scales, glabrous to densely pubescent. Leaves alternate, estipulate, simple, petiolate, chartaceous to coriaceous, often reddish on young shoots, densely to sparsely covered with peltate scales or swollen-headed hairs on both surfaces, often with unicellular hairs on major veins or densely covering abaxial surface, occasionally papillose or glaucous below; margin entire to irregularly and obscurely toothed, strongly

*Continued from Volume 62, page 128.

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toothed, or serrulate; venation brochidodromous to eucamptodromous with midvein prominent and 3° veins reticulate to percurrent; petiole vascular bundle usually bifacial. Inflorescences axillary, racemose, fasciculate, or paniculate, with each flower perfect, 4- to 7- (or 8-)merous, usually fragrant, in axil of small to large, leaflike bract, with 2 often caducous, lateral bracteoles at or near base of pedicel. Calyx of 4 to 7 (or 8) variously aestivated lobes, usually articulate with pedicel, usually persistent in fruit; corolla cylindrical or urceolate (less commonly campanulate or cylindrical with swollen base), with 4 to 7 (or 8) short, imbricate lobes, white to red, very sparsely to densely covered with peltate scales or swollen-headed hairs (rarely also with few unicellular hairs) on abaxial surface, glabrous on adaxial surface; stamens 8 to 14 (to 16) in 2 whorls, inserted at base of corolla, the filaments flattened, geniculate, roughened, papillose or with long, unicellular hairs, strongly expanded near base, with or without pair of short, spurlike appendages below anther-filament junction, the anthers \pm ovoid, papillose, lobes parallel, lacking apical awns, dehiscing by large, introrse-terminal, elliptic pores, always with white line of disintegration tissue on back of each lobe extending at least along apex of filament and along distal edge of spurs, when present, the pollen tricolporate, surface psilate, indistinctly tectate, in tetrads, without viscin strands; stigma truncate to capitate, obscurely 4- to 7- (or 8-)lobed, minutely papillose, the style columnar, usually at least slightly swollen near base, straight, with 4- to 8-fluted central canal, impressed into apex of ovary and included to slightly exserted, the ovary superior, 4- to 7- (or 8-)locular, glabrous to densely covered with unicellular hairs, peltate scales, or swollen-headed hairs, with placentae axile, positioned subapically to nearly basally on columella, slightly bilobed, bearing numerous anatropous ovules, the nectariferous disc an enlargement of base of ovary wall, variously developed and lobed. Capsules loculicidal, subglobose to ovoid, ellipsoid, or urn shaped, with 4 to 7 (or 8) pale, thickened sutures sometimes separating from valves in dehiscence, the placentae persistent on columella. Seeds very small, brown, oblong-ovoid to linear or spindle shaped, the ends sometimes truncated or with sterile extensions or "tails," the testa loose, thin, composed of single layer of very much elongated, thin-walled cells; embryo small, straight, \pm allantoid, white, with 2 small cotyledons, central in cross section, nearer micropylar end, surrounded by fleshy endosperm. Germination epigeal. $2n = 24$.

DISTRIBUTION. Eastern Asia (Japan to Pakistan, south to Malay Peninsula), Greater Antilles (including St. Thomas), and North America (eastern United States and Mexico).

NUMBER OF SPECIES (TAXA). 35 (51).

MEASUREMENTS AND TERMINOLOGY

All measurements (except plant height, which was recorded in the field or taken from information included on specimen labels, and leaf thickness,

which was measured on thin sections of leaves previously softened in water) included in the descriptions of species have been taken directly from dried herbarium material. The width of the calyx lobes was measured midway between the apex and the point where they join with the adjacent lobes; the width of all other structures was measured at the widest point. All drawings of flowers, stamens, anthers, vegetative rhizomes, and petiole and lamina anatomy were made either from material preserved in FAA or from herbarium material previously expanded and softened by boiling in water with a detergent solution. Drawings of capsules (except for cross sections, which were made from material preserved in FAA), seeds, leaves, and buds were made from dried material.

As used here, "glabrous" and "pubescent" refer to the presence or absence of unicellular hairs; the presence, distribution, and density of multicellular hairs is described separately. The indumentum of the buds is only mentioned if it differs from that of the stems.

The anatomic variation in the taxa examined has already been treated in the section concerning vegetative anatomy and in TABLE 8.

SPECIMENS EXAMINED

In the citation of herbarium specimens, abbreviations of institutions follow the sixth edition of *Index Herbariorum* (Holmgren & Keuken, 1974). Specimens are also cited from the private herbarium of Dr. José de Js. Jiménez in Santiago de los Caballeros, Dominican Republic (hereafter referred to as HJ), and from the recently established herbarium of the Jardín Botánico Nacional, "Dr. Rafael M. Moscoso," Santo Domingo, Dominican Republic (hereafter abbreviated as JBM).

In order to conserve space, ordinarily only about 5 to 10 specimens per state have been cited for species in the United States. Similarly, only selected specimens have been cited for species of Mexico, the West Indies, and eastern Asia. Specimens cited are arranged geographically by country and, within the larger countries, by state or province, as follows: United States (Maine, New Hampshire, Vermont, Massachusetts, Rhode Island, Connecticut, New York, New Jersey, Pennsylvania, Delaware, Maryland, District of Columbia, Virginia, West Virginia, North Carolina, South Carolina, Georgia, Florida, Ohio, Kentucky, Tennessee, Alabama, Mississippi, Missouri, Arkansas, Louisiana, Oklahoma, Texas); Mexico (Nuevo León, Tamaulipas, San Luis Potosí, Hidalgo, Puebla, Veracruz, Guerrero, Oaxaca, Chiapas); Cuba (Pinar del Río, Isla de Pinos, Las Villas, Oriente); Haiti; Dominican Republic; Puerto Rico; U. S. Virgin Islands (St. Thomas); Japan (Northern Honshu, Central Honshu, Western Honshu, Shikoku, Kyushu); Taiwan; China (Kiangsu, Anhwei, Chekiang, Kiangsi, Fukien, Kwangtung, Hainan, Honan, Hupeh, Hunan, Kweichow, Kwangsi, Szechwan, Yunnan, Tibet); Vietnam; Laos; Cambodia; Thailand; Malaysia; Burma; Bhutan; Nepal; Bangladesh; India (Arunachal Pradesh, Assam, Nagaland, Manipur, Mizoram, Tripura, Maghalaya, Sikkim, West Bengal, Bihar, Uttar Pradesh, Himachal Pradesh, Punjab, Kashmir); and Pakistan.

1. KEY TO SECTIONS OF LYONIA, INCLUDING SPECIES OF SECTS.

ARSENOCOCCUS AND MARIA

1. Abaxial surface of leaves, pedicels, and calyx lepidote. sect. LYONIA (for species see Key 3).
1. Abaxial surface of leaves, pedicels, and calyx essentially glabrous or pubescent, but not lepidote.
 2. Inflorescences subpaniculate (i.e., racemes of fascicles) or racemose; abaxial leaf surface with scattered, multicellular, extremely long-headed hairs.
 3. Leaves entire; inflorescences racemose. sect. PIERIDOPSIS (for species see Key 2).
 3. Leaves serrulate; inflorescences subpaniculate. sect. ARSENOCOCCUS; one species, 6. *L. ligustrina*.
 2. Inflorescences fasciculate; abaxial leaf surface with scattered, multicellular, chiefly short-headed hairs. sect. MARIA (two species).
 4. Leaves persistent, rigidly coriaceous, with intramarginal vein; corollas usually pink, swollen at base, 2–5 mm. wide; filaments merely roughened; capsules ovoid to ovoid-globose, apex not constricted to only slightly so. 8. *L. lucida*.
 4. Leaves thinner, deciduous, lacking intramarginal vein; corollas usually white, not swollen at base, 4.5–9 mm. wide; filaments long-pubescent, especially near base; capsules urn shaped, apex usually strongly constricted. 7. *L. mariana*.

2. KEY TO THE SPECIES OF LYONIA SECT. PIERIDOPSIS*

1. Capsules essentially lacking thickened sutures.
 2. Leaves with the apex acute to obtuse or rounded with short mucro, the secondary veins often slightly sinuous, varying in strength and angle of divergence from midvein, the lamina 1.8–4.1 by 0.5–1.7(–2.2) cm.; floral buds generally above vegetative buds; calyx lobes 1–2(–2.4) by 0.7–1.7 mm. 1. *Lyonia compta*.
 2. Leaves with the apex long-acuminate to acuminate, often curved, the secondary veins smoothly arching toward margin, the lamina 3.5–9.5 by 1.4–2.7 cm.; floral buds generally below vegetative buds; calyx lobes 2–2.7 by 0.6–0.8 mm. 2. *L. chapaënsis*.
1. Capsules with slightly to strongly thickened, prominent sutures.
 3. Filaments each with 2 spurs near apex; inflorescences (1.5–)2–16(–30) cm. long. 3. *L. ovalifolia*.
 3. Filaments lacking spurs; inflorescences 0.5–5.5(–7) cm. long.
 4. Calyx lobes (2–)3–5(–6.5) by 0.5–1.8(–2) mm., never lobed or divided; leaf apex rounded-mucronate, or acute to obtuse with small to elongated mucro, rarely short-acuminate; inflorescence axis glabrous to densely pubescent. 4. *L. villosa*.
 4. Calyx lobes 4.5–9(–11) by 1.5–5.5(–7) mm., occasionally lobed or divided; leaf apex usually long-acuminate; inflorescence axis glabrous. 5. *L. macrocalyx*.

*Specimen to be identified must have flowers and capsules (persisting from previous season); otherwise, Key 2a should be used.

2a. KEY TO THE SPECIES OF LYONIA SECT. PIERIDOPSIS

1. Inflorescences strongly ascending; flowers pendulous but not secund; floral buds generally above vegetative buds; capsules lacking thickened sutures; leaves persistent *and* with secondary veins \pm irregular and scarcely more prominent than tertiary veins. 1. *Lyonia compta*.
1. Inflorescences usually horizontal to slightly ascending; flowers pendulous and secund; floral buds generally below vegetative buds; capsules with thickened sutures (except in *L. chapaënsis*); leaves deciduous to persistent, the secondary veins irregular or smoothly arching toward margin, usually more prominent than tertiary veins.
 2. Calyx lobes elongated, 1.5–5.5(–7) mm. wide at midpoint, occasionally lobed or divided, abaxial surface papillose; leaves semipersistent, 4–13 cm. long, 2–3.5 times longer than wide, with long-acuminate apices *and* with abaxial surfaces papillose and glaucous; filaments without spurs. 5. *L. macrocalyx*.
 2. Calyx lobes small to elongated, 0.7–1.7(–2.5) mm. wide at midpoint, never lobed or divided, abaxial surface papillose or not, but if papillose, then leaves not long-acuminate; leaves extremely variable but without above combination of characters.
 3. Secondary veins \pm irregular, interconnections often clearly visible.
 4. Filaments lacking spurs; corollas urceolate, globose, or cylindrical; inflorescences (0.5–)1–4(–7) cm. long, often appearing \pm foliaceous-bracted throughout; leaf apices rounded-mucronate, or acute or obtuse with small to elongated mucro, only rarely short-acuminate. 4. *L. villosa*.
 4. Filaments each with 2 spurs near apex; corollas cylindrical; inflorescences (1.5–)2–13(–20) cm. long, usually with few foliaceous bracts near base; leaf apices long- to short-acuminate. 3. *L. ovalifolia* (in part).
 3. Secondary veins smoothly arching toward leaf margin, interconnections often \pm obscure.
 5. Leaves with margin not undulate, the lamina acuminate to short-acuminate, mucronate, acute, or obtuse at apex, with acumen usually shorter and less curved than below; filaments 3–9 mm. long; corollas 5–13 mm. long; capsules with sutures strikingly to slightly thickened, glabrous to occasionally densely short-pubescent (hairs to ca. 0.2–0.3 mm. long). 3. *L. ovalifolia* (in part).
 5. Leaves with margin slightly and irregularly undulate, the lamina usually with long, often curved, acuminate apex; filaments ca. 3 mm. long; corollas 4.5–5.5 mm. long; capsules \pm lacking thickened sutures, moderately to densely pubescent (hairs to ca. 0.5 mm. long). 2. *L. chapaënsis*.

3. KEY TO THE SPECIES OF LYONIA SECT. LYONIA

1. Lamina with a dense covering of unicellular hairs on abaxial surface, or at least with a few such hairs near apex or margin of some leaves.
 2. Leaves with veins prominently and coarsely raised-reticulate (raised ca. 0.2–0.4 mm.) on abaxial surface, petiole and midvein of adaxial surface lacking unicellular hairs, [petiole with medullary bundles within xylem cylinder]; corollas 7–13 mm. wide; capsules 5.5–10.5 mm. wide, 6- or 7-valved.

3. Leaves to ca. 13 cm. long, cuneate to rounded at base, even quaternary and higher order veins slightly depressed on adaxial surface; corollas widely urceolate to campanulate; \pm erect shrub to ca. 6 m. trees. 10. *Lyonia buchii*.
3. Leaves usually not over ca. 6 cm. long, cordate at base (to cuneate in immature plants), quinary and higher order veins \pm obscure on adaxial surface; corollas urceolate; widely branched shrub, usually not over ca. 2 m. 9. *L. heptamera*.
2. Leaves with veins obscure to finely raised-reticulate (raised up to ca. 0.15 mm.) on abaxial surface, petiole and at least extreme proximal portion of midvein of adaxial surface with unicellular hairs, [petiole lacking medullary bundles within xylem cylinder]; corollas 1–6.5 mm. wide; capsules 1–6 mm. wide, mainly 4- and/or 5-valved.
 4. Calyx lobes \pm densely lepidote on both surfaces, 3.5–6 mm. long; corollas always densely lepidote, scales usually yellowish gold. 30. *L. latifolia*.
 4. Calyx lobes abaxially sparsely to densely lepidote, adaxially at most with few scales near margins, 0.5–3(–4) mm. long; corollas sparsely to densely lepidote, the scales rusty to reddish, brownish, or orangish, but not strikingly yellowish gold.
 5. Articulation between pedicel and capsule not developed, pedicel appearing swollen just below capsule; capsules small, very narrowly ovoid, only 1–2 mm. wide, always 4-valved; leaves entire; corollas 2–3 mm. long; calyx lobes 0.5–1 mm. long.
 6. Entire leaf slightly to strongly recurved, the veins, or at least the midvein, often depressed, the lamina obovate to elliptic or narrowly elliptic, ca. 1.5–7 times as long as wide, acute to rounded at apex, adaxial surface often roughened (sometimes obviously so only near margin or apex). . . . 32. *L. glandulosa*.
 6. Leaves flat, the veins not depressed, the lamina orbicular to broadly obovate, less than twice as long as wide, apex always rounded, adaxial surface not roughened. . . . 31. *L. toaënsis*.
 5. Articulation between pedicel and capsule \pm prominent, or at least visible as slight constriction; capsules narrowly to widely ovoid or ellipsoid to subglobose, 1.5–7 mm. wide, 5- and/or 4-valved; leaves entire or obscurely to irregularly toothed; corollas 3–8 mm. long; calyx lobes 0.9–3(–4) mm. long.
 7. Leaves with veins of abaxial surface moderately to strongly, and finely raised-reticulate (secondary through quinary veins raised, although often not visible without magnification), the adaxial surface sometimes rough; capsules \pm narrowly ovoid (to sometimes ovoid in *L. urbaniana*), 1.5–3.5 mm. wide.
 8. Leaves widely ovate to widely elliptic, not much longer than wide, length/width ratio mostly less than 1.6; scales of new growth orangish to orange-brown; corollas 2–4 mm. long; capsules on individual plant 4- (or 4- and 5-)valved, 1.5–2(–2.5) mm. wide. 13. *L. microcarpa*.
 8. Leaves ovate to elliptic, from much longer to ca. slightly less than twice as long as wide, length/width ratio mostly greater than 1.6; scales of new growth tan to \pm dark brown; corollas 3–5.5 mm. long; capsules on individual plant 5- and/or 4-valved, (1.5–)2–3.5 mm. wide.

9. Leaves usually to 3 or 4 cm. long, adaxial surface smooth, abaxial surface usually not densely dark brown lepidote; capsules nearly always 5-valved, elongate-ovoid, usually with slightly constricted apex, the valves slightly S-shaped. 12. *L. tinensis*.
9. Leaves not over ca. 2.5 cm. long, adaxial surface roughened, abaxial surface often densely brownish lepidote; capsules 5- and/or 4-valved, \pm ovoid, the apex not constricted, the valves straight sided or convex. 11. *L. urbaniana*.
7. Leaves with veins of abaxial surface obscure, or if visible, then only slightly or laxly reticulate (higher order veins not raised), the adaxial surface never rough; capsules ovoid or ellipsoid, to subglobose, (2-)2.5-7 mm. wide.
10. Flowers 4-merous; capsules long-ovoid, 2-3 times as long as wide, 2-3(-3.5) mm. wide. 23. *L. elliptica*.
10. Flowers mainly 5-merous (but often 4-merous in *L. alpina*, which has leaves 1-3 by 1-2 cm.); capsules ovoid or ellipsoid to subglobose, 1-2 times as long as wide, 2.5-7 mm. wide.
11. Corollas \pm densely lepidote, long-urceolate; capsules 4-7 mm. wide; calyx lobes 1.2-3(-4) mm. long; leaves entire. 24. *L. nipensis*.
11. Corollas only sparsely lepidote, \pm cylindrical or long-to short-urceolate; capsules 2.5-5(-6) mm. wide; calyx lobes 1-2.5 mm. long; leaves irregularly to obscurely toothed or notched, or entire.
12. Corollas shortly urceolate, 2-5 by 2-4 mm., usually nearly as wide as long; underground rhizomes often produced.
13. Capsules usually subglobose to shortly ovoid, 2.5-4(-5) mm. long; leaf blades \pm flat, the major veins usually not depressed on adaxial surface, the scales of abaxial surface \pm persistent, often dark orange; [montane regions; most individuals lacking unicellular hairs on abaxial leaf surface]. 33. *L. squamulosa* (in part).
13. Capsules ovoid, oblong-ovoid, or ellipsoid, 3-6 mm. long; leaf blades \pm flat to strongly recurved, major veins not depressed to strongly so, scales of adaxial surface deciduous to persistent [Coastal Plain].
14. Flowering branches rigidly ascending, flowers frequent on present year's branchlets (although some flowers also borne on branches of previous year), with leaves conspicuously reduced toward branch tips; leaves \pm flat, the major veins not depressed, the scales of abaxial surface usually all large and erose, often deciduous; small shrub to 1.5(-3) m. tall. 35. *L. fruticosa* (in part).

14. Flowering branches more laxly held, flowers nearly always restricted to previous year's branches, leaves not conspicuously reduced toward branch tips; leaves \pm flat to strongly recurved, major veins usually depressed, often with scales of 2 sizes (large and \pm erose, and smaller, more nearly entire), at least smaller scales \pm persistent, or all scales \pm large and persistent; shrub or small tree to ca. 6(-10) m. tall. 34. *L. ferruginea*.
12. Corollas cylindrical or occasionally long-urceolate, 4-8 by 2-5 mm., always clearly longer than wide; underground rhizomes not produced.
15. Leaves with the secondary veins on adaxial surface more prominent than tertiary and higher order veins, usually clearly joining together in series of arches, the abaxial surface with secondary veins \pm visible and connected together; [inner periclinal walls of adaxial leaf epidermis strongly lignified and thickened]. 22. *L. affinis*.
15. Leaves with the secondary veins on adaxial surface not much more prominent than tertiary or higher order veins, so not clearly joined together in series of arches, or all veins \pm obscure, the abaxial surface with secondary veins obscure to slightly visible, interconnections nearly always obscure; [inner periclinal walls of adaxial leaf epidermis lignified, but no thicker than other epidermal walls].
16. Leaves with the apex acuminate to acute, or rounded-truncate, the abaxial surface with tertiary and higher order veins visible and slightly reticulate; capsules ellipsoid to widely so, 3.5-6 mm. wide. 18. *L. rubiginosa* (in part).
16. Leaves with the apex acute to truncate, usually not acuminate, the abaxial surface with tertiary and higher order veins obscure to very slightly reticulate; capsules ovoid or ellipsoid to subglobose, 3-4.5(-5) mm. wide.
17. Capsules subglobose or globose to short-ovoid, 3-4 mm. long and wide, 4- and 5-valved; leaves strongly coriaceous, ca. 0.5-0.6 mm. thick, \pm densely lepidote beneath. 14. *L. alpina*.
17. Capsules ovoid to ellipsoid, (3-)4-6.5 by 3-4.5(-5) mm., almost exclusively 5-valved; leaves less coriaceous, ca.

- 0.3–0.4 mm. thick, only sparsely or moderately lepidote beneath.
 15. *L. truncata*.
1. Lamina completely lacking unicellular hairs on abaxial surface (although they may be present on midvein or some secondary veins).
18. Margin of distal half of leaves definitely and \pm irregularly toothed.
19. Flowers exclusively 4-merous; lamina rounded to widely cuneate or slightly cordate at base, thinly coriaceous, ca. 0.15–0.2 mm. thick, ca. 2–5.5 cm. wide. 29. *L. maestrensis*.
19. Flowers 5- (rarely 4-)merous; lamina narrowly to widely cuneate (to rounded) at base, moderately to strongly coriaceous, ca. 0.2–0.45 mm. thick, ca. 1–4 cm. wide (but if flowers 4-merous, then only 1–3 cm. wide).
20. Corollas shortly urceolate, 3.5–4.5 mm. long, about as wide as long; capsules subglobose to globose or nearly so, moderately to densely pubescent; young stems glabrous to sparsely pubescent. 16. *L. alainii* (in part).
20. Corollas \pm cylindrical, 4.5–10 mm. long, longer than wide; capsules usually ellipsoid to ovoid, usually only sparsely pubescent; young stems glabrous to densely pubescent.
21. Young stems thick, 2–3.5 mm. wide near base of flowering or fruiting branches, wider in vigorous young shoots, densely pubescent; capsules 3–5 mm. wide, 5-valved; leaves coriaceous, ca. 0.35–0.45 mm. thick.
 17. *L. tuerckheimii*.
21. Young stems thinner, 1.2–2.3 mm. wide near base of flowering or fruiting branches, wider in vigorous young shoots, usually nearly glabrous or only sparsely pubescent; capsules 1.7–3.5(–4.5) mm. wide, 5- and/or 4-valved; leaves thinner, ca. 0.2–0.35 mm. thick.
 18. *L. rubiginosa* (in part).
18. Margin of distal half of leaves entire to undulate or very obscurely toothed.
22. Capsules narrowly ovoid, 1.7–3(–3.5) mm. wide, mainly 4-valved (although rare individuals with mainly 5-valved capsules occur in *L. myrtilloides*); corollas 2.5–4.5 mm. long; petioles 1.5–6 mm. long.
23. Leaves often uniformly small on strongly ascending branches, often obovate, to elliptic or widely elliptic, secondary veins \pm irregular and often very obscure on abaxial surface, apex rounded to truncate; pedicels 2.5–11 mm. long.
 28. *L. myrtilloides*.
23. Leaves not uniformly small on strongly ascending branches, \pm elliptic to ovate, secondary veins \pm regular and \pm apparent on abaxial surface, apex acuminate or acute to rounded or truncate; pedicels 1.5–4.5 mm. long.
24. Capsules long-ovoid, 2.5–5 mm. long, length/width ratio of valves 3–4; young twigs sparsely to densely pubescent; corollas 3–4.5 mm. long. 21. *L. trinidadensis*.
24. Capsules very shortly ovoid, 2.5–4.3 mm. long, length/width ratio of valves 2–3.3; young twigs essentially glabrous; corollas 2.5–4 mm. long. 20. *L. octandra*.

22. Capsules ellipsoid or ovoid, to subglobose, (2.5-)3-6 mm. wide, mainly 5-valved (usually 4-valved in *L. ekmanii*, which has ovoid capsules 4-4.5 mm. wide); corollas 2.5-7 mm. long; petioles 1.5-15 mm. long.
25. Corollas shortly urceolate, 2.5-5 by 2.5-4 mm., as wide as long or nearly so; capsules subglobose to globose or ovoid, 2.5-5 mm. long and wide.
26. Leaves coriaceous, ca. 0.34-0.44 mm. thick, not flexible or only slightly so when dried, not markedly reduced in size toward ends of branches, the margin usually obscurely toothed or notched (or clearly toothed), the apex acute to rounded or truncate but never acuminate, the scales of abaxial surface \pm widely spaced, with margins entire to undulate; neither elongated woody burl nor rhizomes present. 16. *L. alainii* (in part).
26. Leaves thinner, ca. 0.17-0.27 mm. thick, more flexible, sometimes markedly reduced in size toward ends of branches, the margin usually entire or undulate, occasionally obscurely toothed, the apex acuminate or acute to rounded, the scales of abaxial surface widely spaced to overlapping, with margins \pm undulate to erose; elongated woody burl and often rhizomes present.
27. Capsules usually subglobose to shortly ovoid; leaves only sometimes quite strongly reduced in size toward flowering branch tips, the abaxial surface with \pm persistent peltate scales; [montane taxon] 33. *L. squamulosa* (in part).
27. Capsules ovoid to ellipsoid; leaves always \pm conspicuously reduced in size toward ends of rigidly ascending flowering branches, the abaxial surface with \pm deciduous scales; [Coastal Plain taxon; most individuals have a dense covering of unicellular hairs on abaxial leaf surface] 35. *L. fruticosa* (in part).
25. Corollas cylindrical to long-urceolate, 4-7 by 2-4.5 mm., always longer than wide; capsules ovoid to ellipsoid, 3.5-9 by 2.5-6 mm.
28. Calyx lobes 1.3-2.5(-3) mm. long; corollas long-urceolate; capsules 3.5-9 by 3.5-6 mm.; leaves rounded or truncate to acute or nearly so at apex, at least proximal portion of abaxial midvein sometimes with unicellular hairs; filaments usually with 2 minute spurs near junction with anthers.
29. Capsules \pm ovoid with straight-sided valves; pedicels 8-30 mm. long; leaves with abaxial surface sparsely lepidote, with ca. 10 to 40 \pm entire-margined scales/5 sq. mm., the petiole 1.5-5(-9) mm. long. 25. *L. obtusa*.
29. Capsules \pm ellipsoid to ovoid with usually convex valves; pedicels 4-12 mm. long; leaves with abaxial surface moderately lepidote, with ca. 60 to 140 more irregularly margined scales/5 sq. mm., the petiole 4-15(-18) mm. long.

30. Twigs densely pubescent; flowers 5-merous; capsules 4.5–8.5 mm. long. 26. *L. macrophylla*.
30. Twigs essentially glabrous; flowers mainly 4-merous; capsules 3.5–5 mm. long. 27. *L. ekmanii*.
28. Calyx lobes 0.6–2 mm. long; corollas usually \pm cylindrical; capsules 3.5–6 by 2–4 mm.; leaves acute or acuminate to rounded or truncate at apex, abaxial midvein lacking unicellular hairs; filaments lacking spurs.
31. Young twigs usually only sparsely pubescent; leaves with length/width ratio of 1.5–2.5(–3.5), margin obscurely and irregularly toothed to \pm entire, secondary veins sometimes slightly depressed; corollas 4–6 mm. long; [cloud forests]. 18. *L. rubiginosa* (in part).
31. Young twigs usually moderately pubescent; leaves with length/width ratio of 2–4, margin entire or nearly so, secondary veins almost never depressed; corollas (4–) 4.5–7 mm. long; [mainly dry slope forest and thickets]. 19. *L. jamaicensis*.

The following supplementary keys to the species and varieties of *Lyonia* in Cuba, Hispaniola, Jamaica, and continental North America are included as an aid to those interested in the floras of these areas.

4. KEY TO THE SPECIES OF LYONIA IN JAMAICA

1. Flowers 4-merous, corolla 2.5–4 mm. long; capsules 2.5–4.3 by 2–3 mm.; pedicels up to 4 mm. long; young twigs essentially glabrous; [cloud forests and elfin woodlands, ca. (1230–)1450–2250 m. alt.]. 20. *L. octandra*.
1. Flowers 5-merous, corolla (4–)4.5–7 mm. long; capsules 4–6(–7) by 3–4 mm.; pedicels up to 11 mm. long; young twigs sparsely to densely pubescent; [mainly dry slope forests, ca. 150–1300 m. alt.]. 19. *L. jamaicensis*.

5. KEY TO THE SPECIES AND VARIETIES OF LYONIA IN HISPANIOLA

1. Leaves with a dense covering of unicellular hairs on abaxial surface or some leaves at least with few such hairs near apex or margin.
2. Leaves with coarsely raised-reticulate veins on abaxial surface, petiole and midvein of adaxial surface glabrous; corollas carnosae, 7–13 mm. wide; calyx lobes (2–)2.5–6 mm. long; capsules 5.5–10.5 mm. wide, 6- or 7-valved.
3. Leaves to ca. 13 cm. long, cuneate to rounded at base, even quaternary and higher order veins slightly depressed and clearly evident on adaxial surface; corollas widely urceolate to campanulate; \pm erect shrub to medium-sized tree to ca. 6 m. tall; [thickets, cloud forests, and pine forests; 800–2100 m. alt.]. 10. *L. buchii*.
3. Leaves usually not over ca. 5 cm. long, cordate at base (to cuneate in immature plants), quinary and higher order veins \pm obscure on adaxial surface; corollas urceolate; widely branched shrub usually under ca. 2 m. tall; [pine forests, 2000–3175 m. alt.]. 9. *L. heptamera*.
2. Leaves with veins obscure to finely raised-reticulate on abaxial surface, petiole and at least extreme proximal portion of midvein of adaxial surface pubescent; corollas not carnosae, 1.8–4.5 mm. wide; calyx lobes

- 0.8–2 mm. long; capsules 1.5–5 mm. wide, 4- or 5-valved.
4. Capsules ovoid or ellipsoid to subglobose, 3–4.5(–5) mm. wide; corollas 4–7 mm. long; leaves with abaxial surface \pm obscurely veined, to rarely very slightly and laxly reticulate, adaxial surface \pm smooth, lacunae usually not present in cross section (use lens!).
5. Capsules globose to subglobose or shortly ovoid, 3–4 by 3–4 mm., 4- and 5-valved; leaves strongly coriaceous, ca. 0.5–0.6 mm. thick, abaxial surface \pm densely lepidote; [Massif de la Selle, above ca. 2500 m.] 14. *L. alpina*.
5. Capsules ovoid to ellipsoid, (3–)4–6.5 by 3–4.5(–5) mm., almost exclusively 5-valved; leaves thinner, ca. 0.3–0.4 mm. thick, abaxial surface sparsely to moderately lepidote.
6. Leaves 0.8–3.5(–4) cm. long, erect and concave to spreading and \pm flat, sometimes slightly recurved; shrub to 2.5(–3) m. tall, often densely branched; [Sierra de Baoruco and Massif de la Selle, ca. 400–1700 m. alt.] 15a. *L. truncata* var. *truncata*.
6. Leaves (2.5–)3–5(–6.8) cm. long, more spreading and usually \pm flat to recurved; shrub to small tree often to 3–7 m. tall, branching more open and lax; [Cordillera Central and Massif du Nord, ca. 100–1250 m. alt.] 15b. *L. truncata* var. *montecristina*.
4. Capsules \pm narrowly ovoid (to ovoid in *L. urbaniana*), 1.5–3.5 mm. wide; corollas 3–5.5 mm. long; leaves with abaxial surface usually moderately to strongly and finely raised-reticulate, adaxial surface sometimes rough, lacunae usually present in cross section.
7. Leaves broadly ovate to broadly elliptic, length/width ratio mostly less than 1.6; scales of new growth orangish to orange-brown; corollas 3–4 mm. long; capsules on single plant 4- (or 4- and 5-)valved, 1.5–2(–2.5) mm. wide; [Massif de la Selle and Sierra de Baoruco] 13. *L. microcarpa*.
7. Leaves ovate to elliptic, length/width ratio mostly greater than 1.6; scales of new growth usually tan, brown, or dark brown; corollas 3–5.5 mm. long; capsules on single plant 5- and/or 4-valved, (1.5–)2–3.5 mm. wide.
8. Leaves usually to 3–4 cm. long, the adaxial surface \pm smooth, the abaxial surface usually sparsely to moderately lepidote, scales tan to light brown; capsules nearly always 5-valved, elongate-ovoid, apex usually slightly constricted, valves slightly S-shaped; [pine forests of Cordillera Central, ca. 1100–1700 m. alt.] 12. *L. tinensis*.
8. Leaves not over ca. 2.5 cm. long, the adaxial surface rough, the abaxial surface often densely lepidote, scales dark brown; capsules 5- and/or 4-valved, \pm ovoid, apex not constricted, valves straight sided or convex; [pine forests of Cordillera Central, ca. 2000–2400 m. alt.] 13. *L. urbaniana*.
1. Leaves completely lacking unicellular hairs on abaxial surface (although sometimes pubescent on proximal portion of midvein).
9. Corollas 3.5–4.5 mm. long, urceolate, about as wide as long; capsules subglobose to globose or nearly so; young stems glabrous or only sparsely pubescent; margins of leaves obscurely to irregularly toothed. 16. *L. alainii*.

9. Corollas 5.5–10 mm. long, cylindrical, longer than wide; capsules usually ellipsoid or ovoid; young stems nearly glabrous to densely pubescent; margins of leaves more conspicuously toothed.
10. Young stems thick, 2–3.5 mm. wide near base of flowering or fruiting branches (wider in vigorous young shoots), usually densely pubescent; capsules 3–5 mm. wide, 5-valved; leaves coriaceous, 0.35–0.45 mm. thick; [pine forests and thickets, (1700–)2000–3175 m. alt.] 17. *L. tuerckheimii*.
10. Young stems thinner, 1.2–2.3 mm. wide near base of flowering or fruiting branches (wider in vigorous young shoots), at most sparsely pubescent; capsules 1.7–3.5 mm. wide, 5- and/or 4-valved; leaves thinner, 0.2–0.25 mm. thick; [cloud forests, thickets, and pine forests; ca. 900–2100 m. alt.] 18a. *L. rubiginosa* var. *costata*.

6. KEY TO THE SPECIES AND VARIETIES OF LYONIA IN CUBA

1. Leaves with intramarginal vein, the abaxial surface with stalked, glandular-headed hairs. 8. *L. lucida*.
1. Leaves lacking clearly defined intramarginal vein, the abaxial surface lepidote, with scales \pm ferruginous, peltate.
2. Leaves with abaxial surface densely covered with unicellular hairs or at least with a few such hairs near apex or margin.
3. Articulation between pedicel and capsule absent; corollas 2–3 mm. long; calyx lobes 0.5–1 mm. long; capsules very narrowly ovoid, 1–2 mm. wide, always 4-valved.
4. Leaves flat, the veins not depressed, the lamina orbicular to broadly obovate, length/width ratio 0.9–1.8, apex always rounded; [rare; mountains near Toa]. 31. *L. toaënsis*.
4. Leaves slightly to strongly recurved, at least the midvein depressed, the lamina obovate to elliptic or narrowly elliptic, length/width ratio 1.5–7, apex acute to rounded.
5. Leaves obovate (to elliptic), 0.5–2 cm. wide, 1.5–3(–3.5) times as long as wide, the distal margin plane, sometimes slightly revolute; [Sierra de Nipe]. 32a. *L. glandulosa* var. *glandulosa*.
5. Leaves elliptic to narrowly so, usually not over ca. 1 cm. wide, 2.5–7(–10) times as long as wide, distal margin slightly to strongly revolute; [predominantly in Sierra de Micara, Sierra de Cristal, Sierra de Moa, and near Moa] 32b. *L. glandulosa* var. *revolutifolia*.
3. Articulation between pedicel and capsule present; corollas 3.5–8.5 mm. long; calyx lobes 1–6 mm. long; capsules ovoid to widely so, or ellipsoid, always greater than 2 mm. wide, 5- and/or 4-valved.
6. Calyx lobes densely lepidote on both surfaces, 3.5–6 mm. long; corollas always densely lepidote; scales yellowish gold; [chiefly in Sierra Maestra, ca. 650–2000 m. alt.]
7. Leaves with secondary veins at least slightly depressed, the lamina ovate to elliptic or nearly orbicular, length/width ratio 1–1.9, base rounded, slightly cordate, or widely cuneate, the petiole 4–12 mm. long; [Sierra Maestra from Loma del Gato westward]. 30a. *L. latifolia* var. *latifolia*.
7. Leaves with secondary veins not depressed, the lamina elliptic

- to obovate or ovate, length/width ratio (1.2-)1.4-2.4(-2.7), base narrowly to widely cuneate or less commonly rounded, sometimes decurrent, the petiole 8-20 mm. long; [Sierra Maestra from Loma del Gato east to Gran Piedra range and mountains of eastern Oriente] 30b. *L. latifolia* var. *calycosa*.
6. Calyx lobes sparsely to densely lepidote on abaxial surface, at most sparsely lepidote near margins on adaxial surface, lobes 1-3(-4) mm. long; corollas sparsely to densely lepidote; scales rusty to reddish or brownish.
8. Capsules 2-4.5 mm. wide, ovoid to ellipsoid, the valves 4 or 5, convex to straight; corollas sparsely lepidote, \pm cylindrical; scales of pedicel and calyx lobes pale orange; leaf base usually cuneate to decurrent (to widely cuneate or rounded when flowers 4-merous).
9. Flowers 4-merous, corolla 2.5-3 mm. wide; capsules long-ovoid, 2-3(-3.5) mm. wide, at least twice as long as wide; [rare and poorly known] 23. *L. elliptica*.
9. Flowers 5-merous, corolla (2.5-)3-5 mm. wide; capsules ovoid to \pm ellipsoid, 3-4.5 mm. wide, from slightly longer than wide to twice as long as wide; [locally common in Sierra Maestra, ca. 400-700 m. alt.] 22. *L. affinis*.
8. Capsules 4-7 mm. wide, ovoid, the valves 5, straight; corollas densely lepidote, usually \pm long-urceolate; scales of pedicel and calyx lobes orange to deeply orange-red or brownish; leaf base rounded to widely cuneate or slightly cordate.
10. Leaves with blade \pm flat, midvein not depressed to slightly so, secondary veins not depressed, scales of abaxial surface usually irregular margined and deciduous, petiole (2.5-)3-7.5 mm. long; [northern Oriente from Sierra de Nipe to plateau near Moa] 24a. *L. nipensis* var. *nipensis*.
10. Leaves with blade usually strongly recurved, the midvein and secondary veins depressed, often strongly so, the scales of abaxial surface of 2 distinct types (some irregular margined and deciduous, smaller ones \pm entire and persistent), the petiole 1.5-4 mm. long; [Sierra de Moa and Sierra de Toa only] . . . 24b. *L. nipensis* var. *depressinerva*.
2. Leaves with abaxial surface completely lacking unicellular hairs (although such hairs may be present on midvein or some secondary veins).
11. Leaves with margin irregularly toothed, often nearly to base; capsules 4-valved; [little known; Sierra Maestra] 29. *L. maestrensis*.
11. Leaves with margin entire to undulate or obscurely toothed (if toothed, teeth only extending from near apex to ca. midpoint of leaf, never present along margin of proximal half); capsules 4- and/or 5-valved.
12. Capsules 3.5-6.5 mm. wide, ellipsoid to ovoid or widely ovoid, 5-valved (but usually 4-valved in *L. ekmanii*); calyx lobes 1.3-2.5(-3) mm. long; corollas 4-7 mm. long; petioles 2-15 mm. long.
13. Capsules ovoid, valves straight; pedicels 8-30 mm. long; leaves with abaxial surface sparsely lepidote, scales ca.

- 10 to 40/5 sq. mm. and \pm entire; petioles 1.5–5(–9) mm. long.
14. Leaf blades to ca. 7 cm. long, usually slightly to strongly recurved, often with midvein and/or secondary veins depressed, abaxial surface with tertiary veins much less prominent than secondary veins and obscure to slightly reticulate, apex predominantly rounded; [Moa-Baracoa region]. 25a. *L. obtusa* var. *obtusa*.
14. Leaf blades to ca. 3.5 cm. long, \pm flat, veins not depressed, abaxial surface with tertiary veins nearly as prominent as secondary veins and strongly reticulate, apex acute to rounded; [Sierra de Cristal].
. 25b. *L. obtusa* var. *longipes*.
13. Capsules \pm ellipsoid to ovoid, valves \pm convex; pedicels 4–12 mm. long; leaves with abaxial surface moderately lepidote, scales ca. 60 to 140/5 sq. mm. and more irregular margined, petiole 4–15(–18) mm. long.
15. Twigs densely pubescent; flowers 5-merous; capsules 4.5–8.5 mm. long; [common; mountains of northern Oriente from Sierra de Nipe to Moa-Baracoa region]. 26. *L. macrophylla*.
15. Twigs essentially glabrous; flowers mainly 4-merous; capsules 3.5–5 mm. long; [rare; Pinar del Río].
. 27. *L. ekmanii*.
12. Capsules 1.7–3(–3.5) mm. wide, narrowly ovoid, mainly 4-valved (very rarely 5-valved in *L. myrtilloides*); calyx lobes 0.7–1.5 mm. long; corollas 2.5–4.5 mm. long; petioles 1.5–5.5 mm. long.
16. Leaves obovate, sometimes elliptic or widely so, often uniformly small on strongly ascending branches, the secondary veins \pm irregular, often very obscure on abaxial surface, the apex rounded to truncate; pedicels 2.5–11 mm. long; filaments with minute spurs; [pinelands and savannas, Pinar del Río and Isle of Pines]. . . . 28. *L. myrtilloides*.
16. Leaves \pm elliptic to ovate, not uniformly small on strongly ascending branches, the secondary veins \pm regular, usually evident, the apex acuminate to acute, truncate, or rounded; pedicels 2.5–4.5 mm. long; filaments lacking spurs; [cloud forests and savannas, Sierra de Trinidad and Sierra de Sancti Spiritus of Las Villas Prov.]. 21. *L. trinidadensis*.

7. KEY TO THE SPECIES AND VARIETIES OF LYONIA IN CONTINENTAL
NORTH AMERICA

1. Abaxial surface of leaves, pedicels, and calyx lepidote.
2. Leaves with abaxial surface usually glabrous but \pm persistently lepidote, lamina \pm flat, major veins usually not depressed on adaxial surface; capsules usually subglobose to shortly ovoid, 2.5–4(–5) mm. long; [Mexico, Sierra Madre Oriental and mountains of Chiapas].
. 33. *L. squamulosa*.
2. Leaves with abaxial surface usually sparsely to densely pubescent and deciduously or persistently lepidote, lamina flat to strongly recurved, major veins not depressed to strongly so; capsules ovoid, oblong-ovoid,

- or ellipsoid, 3–6 mm. long; [Coastal Plain, southeastern United States].
3. Ultimate branchlets rigidly ascending, flowers frequent on present year's branchlets (although some flowers also borne on branches of previous year), with leaves conspicuously reduced toward branch tips; leaves with the distal margin at most slightly revolute, the major veins not depressed, the abaxial surface with scales usually all large and \pm irregular margined, often deciduous; small shrub to 1.5(–3) m. tall. 35. *L. fruticosa*.
 3. Ultimate branches not rigidly ascending, flowers nearly always restricted to previous year's branches, with leaves not conspicuously reduced toward branch tips; leaves with the distal margin usually revolute, sometimes strongly so, the major veins usually depressed, the abaxial surface with some scales often large and irregular margined, others smaller and more nearly entire, at least smaller scales \pm persistent (or all scales \pm large and persistent); shrub or small tree to ca. 6(–10) m. tall. 34. *L. ferruginea*.
 1. Abaxial surface of leaves, pedicels, and calyx nearly glabrous or pubescent, but not lepidote.
 4. Inflorescences subpaniculate; leaves with scattered, multicellular, extremely long-headed hairs on abaxial surface, margin serrulate; corollas urceolate, 2–4.5 mm. long; calyx lobes 0.5–1.5 mm. long.
 5. Inflorescences naked or with only few foliaceous bracts; [chiefly on mountains and Piedmont south of Virginia, and mountains, Piedmont, and Coastal Plain north of Virginia].6a. *L. ligustrina* var. *ligustrina*.
 5. Inflorescences with conspicuously foliaceous bracts or at least lower inflorescences with large foliaceous bracts; [chiefly on Coastal Plain from southeastern Virginia to Florida, and west to eastern Texas, Oklahoma, and Arkansas (mountains)].6b. *L. ligustrina* var. *foliosiflora*.
 4. Inflorescences fasciculate; leaves with scattered, multicellular, mostly short-headed hairs on abaxial surface, the margin entire; corollas \pm cylindrical, 5–14 mm. long; calyx lobes 2–9.5 mm. long.
 6. Leaves rigidly coriaceous, persistent, with intramarginal vein; corollas usually pink, swollen at base, 2–5 mm. wide; filaments merely roughened; capsules with apex at most slightly constricted. 8. *L. lucida*.
 6. Leaves thinner, deciduous, lacking intramarginal vein; corollas usually white, not swollen at base, 4.5–9 mm. wide; filaments long-pubescent, especially near base; capsules with apex usually strongly constricted. 9. *L. mariana*.

Lyonia Nutt. sect. *PIERIDOPSIS* (Rehder) Airy Shaw, Curtis's Bot. Mag. **160**: t. 9490. 1937.

Pieris D. Don sect. *Eupieris* Bentham & Hooker, Gen. Pl. **2**: 588. 1876, *nomen illegit.*

Xolisma Raf. sect. *Pieridopsis* Rehder, Jour. Arnold Arb. **5**: 55. 1924.
TYPE SPECIES: *Lyonia ovalifolia* (Wallich) Drude.

Deciduous to evergreen shrubs to trees, often spreading by horizontal underground rhizomes, the branches with homogeneous pith. Indumentum

of unicellular hairs and multicellular, biseriate-stalked, extremely long-headed hairs. Buds with 2 large, imbricate scales. Leaves entire, with unligified or only slightly lignified epidermis and lacking hypodermis (except in *L. compta*); abaxial epidermis sometimes papillose and/or glaucous. Flowers in short to elongated racemes, 5-merous; calyx lobes valvate in bud; corolla cylindrical to urceolate; filaments with long, unicellular hairs, especially near base (rarely papillose), and unappendaged or with pair of small to very well developed spurs below junction with anthers. Capsules usually with pale, slightly to strongly thickened sutures, sutures usually adhering to valve or splitting irregularly in dehiscence, sometimes only poorly developed; placenta positioned subapically to centrally on columella; seeds oblong-ovoid to spindle shaped, one end sometimes truncated.

DISTRIBUTION. Asia, from northern Pakistan through Himalayas to western and central China, southern and central Japan, and Taiwan, extending southward into Vietnam, Cambodia, and Thailand, with disjunct populations in Malay Peninsula.

NUMBER OF SPECIES (TAXA). 5 (13).

1. ***Lyonia compta*** (W. W. Sm. & Jeffrey) Hand.-Mazz. Symb. Sin. 7: 790. 1936.

Pieris compta W. W. Sm. & Jeffrey, Notes Roy. Bot. Gard. Edinburgh 9: 116. 1916. *Xolisma compta* (W. W. Sm. & Jeffrey) Rehder, Jour. Arnold Arb. 5: 53. 1924. TYPE: China, Yunnan, vicinity of Yun-nan-sen [Kun-ming Shih], in moist valleys, *E. E. Maire 1071* (lectotype, E!; isolectotypes, E!, K!, UC!).

Evergreen or nearly evergreen shrub to ca. 2 meters tall, with brownish to gray, longitudinally furrowed bark. Twigs terete to slightly angled, slender, with few long-headed hairs, otherwise sparsely to densely pubescent. Buds ovoid to elongate-ovoid, 1–4 by 1–2.5 mm. Leaf blades elliptic to obovate or sometimes ovate, 1.8–4.1 by 0.5–1.7(–2.2) cm., ± flat, coriaceous, ca. 0.23–0.34 mm. thick, apex acute to rounded with short mucro, base broadly cuneate to rounded (sometimes slightly cordate); margin entire, plane to clearly revolute; venation brochidodromous, 3° veins ± reticulate; adaxial surface with sparse long-headed hairs, otherwise ± glabrescent, sparsely to densely pubescent on midvein, both 2° and 3° veins obscure to only slightly visible; abaxial surface with sparse long-headed hairs, otherwise glabrous or sparsely pubescent on sides of midvein near leaf base, the 3° and higher order veins slightly and laxly reticulate, the 2° veins slightly raised and visible, ± irregular and sinuous, not much more prominent than 3° veins; petiole 1.5–5.5 mm. long, with long-headed hairs, otherwise pubescent adaxially or all around. Flower buds usually above vegetative buds; inflorescences racemose, to ca. 35-flowered, (4.5–)6–15 cm. long, rigidly ascending; flowers not secund. Pedicels slender, 3–7 mm. long, with long-headed hairs, otherwise pubescent; bracteoles opposite, basal, triangular to ovate or linear, 0.8–1.8 mm. long; bracts large (often to 1 or 2 cm. long) and leaflike near base of raceme

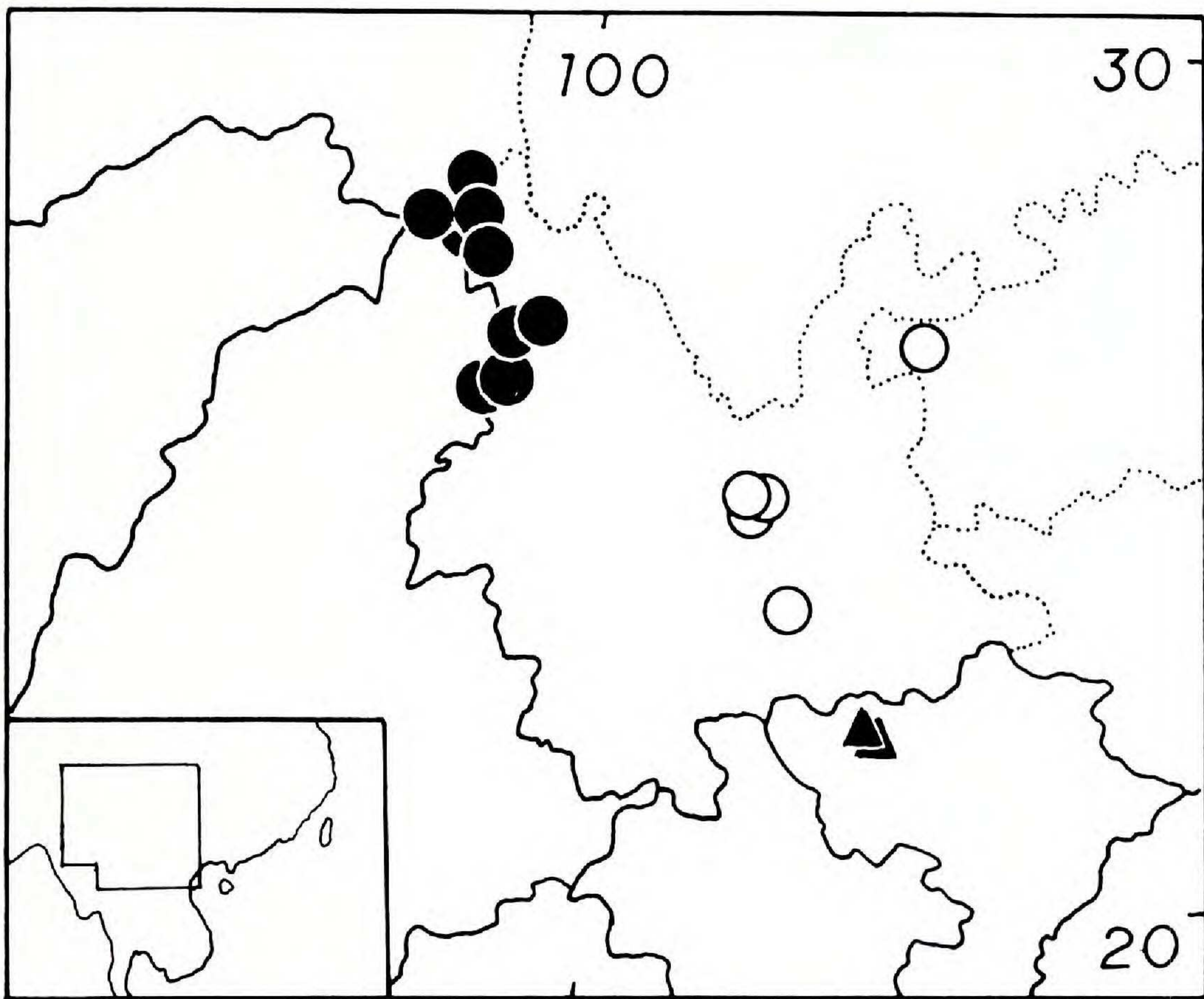
but near apex gradually becoming very small and similar to bracteoles. Flowers usually 5-merous; calyx lobes triangular to triangular-ovate, with acute to acuminate apices, 1-2(-2.4) by 0.7-1.7 mm., the adaxial side with few long-headed hairs near margins, sparsely pubescent near apex, the abaxial side with scattered long-headed hairs, otherwise glabrous to densely pubescent, especially near base; corolla urceolate, 3-4.5(-5.5) by 2.7-4 mm., white, abaxially with moderate to dense long-headed hairs; filaments roughened in upper portion but always with at least few long, unicellular hairs often mixed with small papillae near base, 2-3.5 mm. long, with $2 \pm$ well developed spurs to ca. 0.3 mm. long below anther-filament junction, anthers 1-1.5 mm. long; ovary pubescent, placentae subapical. Capsule short-ovoid or subglobose to globose, 2.7-4 by 3-4(-4.5) mm., \pm lacking long-headed hairs, otherwise moderately to densely pubescent, especially near base, with pale, very poorly developed, at most slightly thickened sutures that in dehiscence split irregularly down middle with portions remaining attached to one or both adjacent valves; seeds 0.8-1.2 mm. long. (FIGURE 20; see also Stevens, 1970.)

DISTRIBUTION AND ECOLOGY. China, Yunnan and Kweichow provinces (MAP 5). Mountainous areas, open pine forests, moist valleys, marshy places, and savannas; over marl and sandstone; ca. 1400-2300 m. alt. (Handel-Mazzetti, 1936). Probably flowering chiefly late May through June.

REPRESENTATIVE SPECIMENS. **China.** KWEICHOW: locality illegible, *Esquirol* 6062 (P). YUNNAN: Yunnan-fu to Tali-fu, Lufong, *Handel-Mazzetti* 8657 (w); vic. of Yun-nan-sen, *Maire* 1874 (E, UC, US); Lo Shuieh Mt., *McLaren's collectors* U104 (A, E); Tsu-Gung, *McLaren's collectors* 162F(aa) (E, UC); Yunnan-fu Distr., Mt. Man-gan, *Schoch* 145 (A, K, US); K'un-ming, *Wang* 62680 (A).

Lyonia compta is a very distinctive species immediately recognizable by its more or less rigidly ascending racemes arising from buds toward the apices of the branches; small, urceolate corollas; usually short-ovoid capsules with only very poorly developed sutures; and usually quite small (to 4 by 1.7 cm.), elliptic to obovate leaves. It is also the only Asian species that has a hypodermis in its leaves. Although it clearly belongs in sect. PIERIDOPSIS, it is probably not closely related to any other Asian taxon. Its capsules are very similar to those of *L. chapaënsis*, but it differs from that species in its more strongly ascending, not secund inflorescences, which are more often leafy bracted and generally arise from floral buds situated above the vegetative buds on the branch. It also differs in its small, urceolate corollas; filaments more commonly with long, unicellular hairs near the base; shorter calyx lobes; and much smaller, differently shaped leaves with an adaxial hypodermis.

Several plants collected by Handel-Mazzetti near Yunnan-fu (13085 (A, E, US, w)) have leaves that are longer than is normal for this taxon, with their secondary veins smoothly arching toward the leaf margin (vs. irregular or sinuous in typical *Lyonia compta*), and the tertiary veins more or less percurrent (vs. reticulate). The leaves also lack the adaxial hypodermis characteristic of *L. compta* but have a more or less discontinuous and slightly lignified layer of cells along their abaxial epidermis. The flowers have quite



MAP 5. Distribution of *Lyonia compta* (Yunnan and Kweichow; circles), *L. chapaensis* (Vietnam; triangles), and *L. ovalifolia* var. *doyonensis* (Yunnan, Tibet, and Burma; dots).

large (to ca. 6 mm. long) corollas and elongate (to ca. 3.5 mm.), acute-tipped calyx lobes; they are borne on pedicels up to 10 mm. long. Finally, the bracts of the racemes do not decrease gradually in size from the base to the apex as is usual in *L. compta*; instead they often have only one to three large, foliaceous bracts near the base, with the other bracts very small and resembling the bracteoles in shape and size. All these characters tend toward the usual condition in *L. ovalifolia* var. *lanceolata*, which is sympatric with *L. compta*. These plants would be just as out of place in the former taxon because they show several features characteristic of *L. compta* (for example, corollas urceolate (vs. cylindrical and to ca. 12 mm. long in *L. ovalifolia* var. *lanceolata*), with a \pm dense covering of long-headed, multicellular hairs; leaves coriaceous and evergreen, to ca. 4.5 mm. long, the apices obtuse to rounded with a small mucro (vs. usually \pm deciduous, to ca. 11 cm. long, with acuminate apices); and inflorescences \pm ascending, often arising near the apex of the branches (vs. \pm horizontal to only slightly ascending, arising from floral buds that are generally below the vegetative buds)). It is probable that these morphologically intermediate specimens represent hybrids between *L. compta* and *L. ovalifolia* var. *lanceolata*.

Since Smith and Jeffrey (1916) did not select a type specimen for the species when it was described but merely listed two collections of E. E. Maire (nos. 1071 and 1874), I have selected the specimen of *Maire 1071* at Edinburgh as the lectotype.

2. *Lyonia chapaënsis* (Dop) Merr. Jour. Arnold Arb. **23**: 188. 1942.

Pieris chapaënsis Dop in Lecomte, Fl. Gén. Indo-chine **2**: 726. 1930. TYPE: Tonkin [Vietnam], Massif de Lo-sui-tong, near Cha-pa, 2200 m. alt., 29 July 1926, *Poilane 12682* (holotype, P!; fragment of holotype, L!).

Pieris chapaënsis Dop var. *glabra* Dop & Trochain, Bull. Mus. Hist. Nat. Paris, ser. 2. **4**: 719. 1932. TYPE: Tonkin [Vietnam], Massif du Tam Dao, [Chapa], 1400 m. alt., May 1931, *Pételot 3214* (holotype, P!; isotypes, A!, NY (2 sheets)!, US (2 sheets)!).

Semi-evergreen shrub or small tree to ca. 4 meters tall, with brownish to gray, longitudinally furrowed bark. Twigs terete to slightly angled, slender, with few long-headed hairs, otherwise glabrous to densely pubescent. Buds elongate-ovoid to ovoid, 1–4 by 1–3 mm. Leaf blades elliptic to slightly obovate or ovate, 3.5–9.5 by 1.4–2.7 cm., ± flat, slightly coriaceous, ca. 0.12–0.24 mm. thick; apex acuminate to extremely long-acuminate and often curved; base narrowly cuneate to rounded; margin entire, plane to slightly revolute, usually irregularly undulate; venation eucamptodromous to slightly brochidodromous (especially toward apex), 3° veins reticulate to slightly percurrent; adaxial surface with sparse long-headed hairs, otherwise ± glabrescent, sparsely to densely pubescent on midvein and also sometimes on 2° veins, with 3° and higher order veins obscure to visible, not depressed to slightly so; abaxial surface with sparse long-headed hairs, otherwise glabrous or sparsely to moderately pubescent on sides of midvein near leaf base, occasionally with few hairs also on 2° veins, the 3° and higher order veins slightly visible, the 2° veins slightly raised and visible, smoothly arching toward margin; petiole 3–11 mm. long, with long-headed hairs, otherwise usually pubescent only adaxially. Flower buds usually below vegetative buds; inflorescences racemose, to ca. 30-flowered, 4–10 cm. long, slightly (occasionally strongly) ascending; flowers pendulous and secund. Pedicels slender, 3–5 mm. long, with long-headed hairs, otherwise pubescent; bracteoles opposite, basal, narrowly triangular to linear, 1–2.6 mm. long; bracts often quite variable, all to ca. 2.5 mm. in length (or sometimes 1 to 3 leaflike ones to ca. 2.5 cm. long near base of raceme). Flowers 5-merous; calyx lobes triangular, with acute, slightly acuminate, or rounded apices, 2–2.7 by 0.6–0.8 mm., the adaxial side with few long-headed hairs (especially near margins), otherwise very sparsely to moderately pubescent, the abaxial side with scattered long-headed hairs, otherwise subglabrous; corolla long-urceolate, 4.5–5.5 by 3–4 mm., white, abaxially with sparse long-headed hairs; filaments roughened-papillose, lacking long-unicellular hairs or with few such hairs near base, ca. 3 mm. long, usually with 2 small spurs to ca. 0.2 mm. long below anther-filament junction, or unappendaged, anthers 1–1.2 mm. long; ovary pubescent, placentae ± subapical. Capsule short-ovoid to subglobose, 2.5–3

by 2.5–3.5 mm., lacking long-headed hairs, otherwise moderately to densely pubescent, with pale, at most very slightly thickened sutures that in dehiscence split irregularly down middle with portions remaining attached to one or both adjacent valves; seeds 1–1.2 mm. long. (FIGURE 20.)

DISTRIBUTION AND ECOLOGY. Vietnam, vicinity of Cha-pa (MAP 5). Mountainous areas, ca. 1400–2200 m. alt. Single flowering specimen known to author (*Pételot* 3214) collected in May.

ADDITIONAL SPECIMENS EXAMINED. **Vietnam:** Massif du Fan tsi Pan, vic. of Cha-pa, *Pételot* 4434 (NY, P).

This interesting and narrowly endemic species is probably only distantly related to the other Asian taxa. It is easily distinguished by its leaves with their often extremely elongated, acuminate apices and slightly and irregularly undulate margins; by its often densely pubescent, short-ovoid capsules with very poorly developed suture thickenings; and by its roughened-papillose filaments that often lack unicellular hairs. *Lyonia chapaënsis*, especially if sterile, may be confused with *L. ovalifolia* vars. *lanceolata* or *rubrovenia* but can be recognized by its leaves, which usually have a distinctive shape and slightly undulate margins, and which lack a lignified layer (or layers) of mesophyll cells near the abaxial surface. Although its capsules are quite similar to those of *L. compta*, these two species differ in many other characters.

3. ***Lyonia ovalifolia*** (Wallich) Drude in Engler & Prantl, Nat. Pflanzenfam. 4(1): 44. 1889.

Deciduous to evergreen shrub to moderate-sized tree to 7.5(–18) meters tall, often with slightly twisted or gnarled trunk and brownish to gray, longitudinally furrowed bark, sometimes spreading vegetatively by horizontal underground rhizomes. Twigs terete or slightly ridged, slender to stout, often with few long-headed hairs, otherwise glabrous to densely pubescent. Buds elongate-ovoid, 1–11.5 by 1–7 mm., often reddish. Leaf blades nearly orbicular, narrowly to widely elliptic, ovate, or obovate, 2.5–15(–21) by 0.8–10(–12) cm., ± flat, chartaceous to quite coriaceous, ca. 0.1–0.33 mm. thick, sometimes turning reddish in autumn, sometimes with 1 or 2 layers of lignified mesophyll cells near abaxial epidermis; apex long-acuminate to rounded with small mucro or obtuse, sometimes curved or folded over in pressing; base narrowly cuneate to cordate; margin entire, plane to slightly revolute; venation brochidodromous to eucamptodromous, 3° veins percurrent to reticulate; adaxial surface with sparse long-headed hairs, otherwise often glabrescent, very sparsely to densely pubescent on midvein, with pubescence sometimes extending to 2°, 3°, or higher order veins, occasionally all veins glabrous, the 3° and higher order veins visible to obscure, occasionally slightly depressed, the 2° veins prominently raised to slightly depressed or nearly obscure; abaxial surface papillose to smooth, glaucous or greenish to shiny yellowish gold, with sparse to dense long-headed hairs, otherwise glabrous or very sparsely to densely pubescent along midvein, with pubescence occasionally extending to adjacent 2° or higher order veins, the 3° and higher order veins visible to obscure,

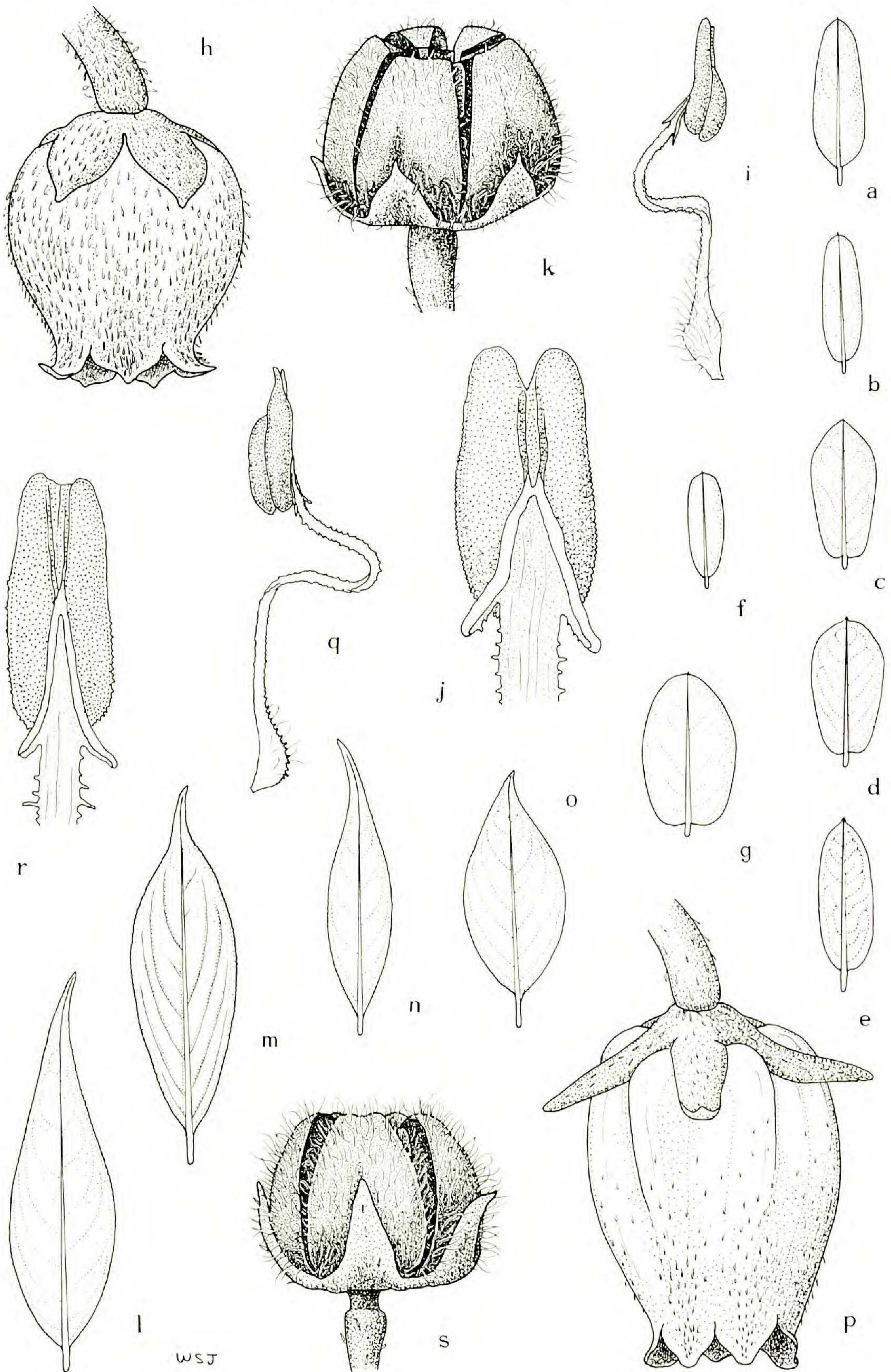


FIGURE 20. a-k, *Lyonia compta*: a-g, leaves, $\times .5$; h, flower, $\times 6$; i, stamen, $\times 12.5$; j, anther, $\times 25$; k, capsule, $\times 6$. l-s, *L. chapaensis*: l-o, leaves, $\times .5$; p, flower, $\times 6$; q, stamen, $\times 12.5$; r, anther, $\times 25$; s, capsule, $\times 6$.

the 2° veins prominently raised and visible to nearly obscure, smoothly arching toward margin to sinuous or irregular and joined together to form series of arches, occasionally drying slightly ferruginous; petiole 2–15(–20) mm. long, with long-headed hairs, otherwise glabrous or pubescent adaxially or all around. Flower buds usually below vegetative buds; inflorescences racemose, to ca. 40- (to 60-)flowered, (1.5–)2–16(–30) cm. long, horizontal to slightly ascending; flowers pendulous and secund. Pedicels slender to stout, (1.5–)2–10 mm. long, with long-headed hairs, otherwise glabrous or ± pubescent; bracteoles opposite, basal, widely triangular to linear, 0.4–2.5(–4) mm. long; bracts extremely variable, 1 to 9 large and leaflike near base of raceme, the others very small, similar to bracteoles in shape, often caducous (occasionally all small and similar to bracteoles in shape). Flowers 5-merous; calyx lobes triangular to nearly linear, with acuminate or acute to rounded apices, 1–5(–6.5) by 0.6–1.9(–2.5) mm., the adaxial side often with few long-headed hairs, otherwise glabrous to densely pubescent, the abaxial side with scattered long-headed hairs, otherwise glabrous or sparsely (rarely densely) pubescent; corolla cylindrical to slightly urceolate, 5–13(–13.5) by 2.5–6.5(–7) mm., white or sometimes slightly pink tinged, especially toward apex, abaxially with sparse to dense long-headed hairs; filaments with long-unicellular hairs, especially near base, 3–9 mm. long, with 2 spurs to ca. 0.2–0.5 mm. long below anther-filament junction, anthers 0.8–1.8 mm. long; ovary glabrous to densely pubescent, placentae subapical to central. Capsule subglobose, globose, short-ovoid, or ovoid, 2.5–5.5 by 2.5–6 mm., very occasionally with few long-headed hairs, otherwise glabrous to densely pubescent, especially near base, with pale, moderately (sometimes only slightly) thickened sutures that in dehiscence usually remain attached to an adjacent valve or split irregularly; seeds 0.7–1.6 mm. long.

DISTRIBUTION. In an arc from Japan westward across China (including Taiwan and Hainan) to northern Pakistan, south to Thailand and Malay Peninsula. Various habitats, 20–3350(–3800) m. alt.

Key to the Varieties of *Lyonia ovalifolia*

1. Secondary veins often slightly sinuous, of varying strengths and angles of divergence from midvein, the connections between secondary veins often clearly visible.
 2. Abaxial leaf surface densely pubescent along secondary veins and sides of midvein, always with dense tuft of long-unicellular hairs in angle between midvein and secondary veins at leaf base; inflorescences (1.5–)2–7(–10) cm. long; corollas 6–8(–9.5) mm. long; leaves 3.5–10.5(–13) cm. long; [Japan and Taiwan]. 3a. var. *elliptica*.
 2. Abaxial leaf surface glabrous to sparsely or densely short-pubescent along secondary veins and midvein, but never with such a tuft of hairs; inflorescences 3–13(–20) cm. long; corollas 6.5–12.5 mm. long; leaves 5–12.5(–16) cm. long; [China].
 3. Leaves longer than wide, 5–12.5(–15) by 2.3–6.5(–8) cm., length/width ratio (1.6–)1.8–3(–3.5), apex usually acuminate to long-acuminate, base obtuse to cordate, blade usually chartaceous to slightly coriaceous, abaxial epidermis not papillose; inflorescence axis glabrous

- to sparsely pubescent; [Kiangsu and Chekiang west to Szechwan and Yunnan, south to Kwangsi and Kwangtung] 3b. var. *hebecarpa*.
3. Leaves as wide as long or nearly so, 6.5–12(–16) by 5.3–10(–12) cm., length/width ratio 0.9–1.3(–1.5), apex abruptly short-acuminate, base rounded to cordate, blade usually quite coriaceous, abaxial epidermis obscurely to clearly papillose; inflorescence axis glabrous; [northwestern Yunnan and adjacent Tibet and Burma] 3c. var. *doyonensis*.
1. Secondary veins smoothly arching toward leaf margin (to rarely slightly irregular in var. *ovalifolia*), their interconnections often obscure.
4. Leaves quite large and as wide as long or nearly so, 6.5–12(–16) by 5.3–10(–12) cm., length/width ratio 0.9–1.3(–1.5), apex truncately short-acuminate, abaxial side with tertiary veins very prominent and epidermis papillose; [northwestern Yunnan and adjacent Tibet and Burma] 3c. var. *doyonensis*.
4. Leaves without above character combination, usually much longer than wide, 2.5–15(–21) by 1–8.5(–11.5) cm., length/width ratio (1.2–)1.4–7, apex long- to short-acuminate, acute, or obtuse, abaxial side with tertiary veins obscure to visible but not prominently raised, and with epidermis often lacking papillae.
5. Leaves usually ovate, with base widely cuneate to rounded or cordate, blade 6–15(–21) by (2–)3.5–8.5(–11.5) cm., length/width ratio (1.2–)1.4–2.4(–2.5), the abaxial epidermis green to glaucous, sometimes papillose, only occasionally yellowish and shiny when dried; capsules usually subglobose; calyx lobes 1.5–2.5 mm. long (but to ca. 3.5 mm. in western Himalayas); inflorescences 3–16(–30) cm. long; lamina with mesophyll cells never lignified; [Pakistan and northwestern India east to Yunnan and Kwangsi, south to Thailand and Malay Peninsula] 3d. var. *ovalifolia*.
5. Leaves elliptic to obovate or ovate, with base usually narrowly cuneate to rounded, blade 2.5–11(–14.5) by 1.2–4.5(–7) cm., length/width ratio (1.5–)1.7–3.5(–7), abaxial epidermis greenish to yellowish green and lustrous when dried, never papillose or glaucous; capsules often short-ovoid to ovoid, less commonly globose to subglobose; calyx lobes (2–)2.5–4.5(–6.5) mm. long; inflorescences 2.5–9(–18) cm. long; lamina with 1 or 2 layers of lignified mesophyll cells near abaxial epidermis.
6. Capsules subglobose to globose, sutures often poorly differentiated from valves; corollas 5–7 mm. long; filaments 3–4 mm. long with spurs 0.1–0.3 mm. long; inflorescences usually lacking foliaceous bracts; [Hainan and Vietnam] 3g. var. *rubrovenia*.
6. Capsules ovoid to short-ovoid, less commonly globose (or subglobose), sutures usually well differentiated from valves; corollas (6–)7–10(–12.5) mm. long; filaments 5–7.5 mm. long with spurs 0.2–0.6 mm. long; inflorescences with at least few large, foliaceous bracts near base.
7. Leaves 2.5–6(–7) cm. long, apex abruptly short-acuminate, to obtuse or rounded with small mucro, petiole 2–8 mm. long; inflorescences with foliaceous bracts often \pm throughout; capsules 2.5–4 mm. long; [Thailand] 3f. var. *foliosa*.
7. Leaves 5–11(–14.5) cm. long, apex acuminate, petiole 5.5–14

mm. long; inflorescences with foliaceous bracts usually limited to base; capsules 3–5(–5.5) mm. long; [China and northern Burma] 3e. var. *lanceolata*.

3a. *Lyonia ovalifolia* (Wallich) Drude var. *elliptica* (Sieb. & Zucc.) Hand.-Mazz. Symb. Sin. 7(4): 788. 1936.

Andromeda elliptica Sieb. & Zucc. Abh. Math.-Phys. Cl. Königl. Bayer. Akad. Wiss. München 4: 126. 1846. *Pieris ovalifolia* (Wallich) D. Don var. *elliptica* (Sieb. & Zucc.) Rehder & Wilson in Sarg. Pl. Wilson. 1: 552. 1913. *Pieris elliptica* (Sieb. & Zucc.) Nakai, Tokyo Bot. Mag. 33: 207. 1919. *Xolisma ovalifolia* (Wallich) Rehder var. *elliptica* (Sieb. & Zucc.) Rehder, Jour. Arnold Arb. 5: 52. 1924. *Xolisma elliptica* (Sieb. & Zucc.) Nakai, Trees Shrubs Japan. ed. 1 (rev.). 204. 1927, non Wright ex Small, 1914. *Lyonia neziki* Nakai & Hara, Jour. Jap. Bot. 14: 336. 1938, *nomen novum*. *Lyonia ovalifolia* subsp. *neziki* (Nakai & Hara) Hara, Fl. East. Himalaya, 648. 1966. TYPE: Japan, locality not specified. Lectotype should be selected from material sent to Siebold by H. Bürger in 1842, and labeled as “*Andromeda (Pieris) elliptica* S. & Z. . . . no. 433” at L, but material at LE must be examined; specimens at L, M, and K seen.

Pieris formosana Komatsu in Matsum. Ic. Pl. Koishikav. 3: 71. t. 181. 1916. *Xolisma formosana* (Komatsu) Nakai, Trees Shrubs Japan. ed. 1 (rev.). 204. 1927. TYPE: Taiwan, Ren-tai-san, *Hayata & Mori s.n.*, 10 Aug. 1908 (lectotype, TI!).

Pieris pilosa Komatsu in Matsum. Ic. Pl. Koishikav. 3: 73. t. 182. 1916. *Xolisma formosana* (Komatsu) Nakai var. *pilosa* (Komatsu) Nakai, Trees Shrubs Japan. ed. 1 (rev.). 204. 1927. TYPE: Taiwan, not seen.

Deciduous shrub to small tree to 6(–12) meters tall. Buds 1–9 by 1–3.5 mm. Leaf blades elliptic, ovate, or less commonly obovate, 3.5–10.5(–13) by 1.8–6(–7.5) cm., mesophyll unligified; apex acute to long-acuminate, sometimes curved, often folded over in pressing; base cuneate, or rounded to cordate; venation brochidodromous, 2° veins sinuous or irregular; abaxial surface neither papillose nor glaucous, densely pubescent along 2° veins and sides of midvein, to almost glabrous, always with dense tuft of long-unicellular hairs along sides of midvein and adjacent 2° veins at leaf base; petiole 4.5–18 mm. long. Inflorescences (1.5–)2–7(–10) cm. long, usually with ca. 1 to 3 large, leaflike bracts to 2–6(–11) cm. long near base. Calyx lobes 1–3.5(–4) by 0.6–1.5 mm.; corolla cylindrical, 6–8(–9.5) by 2.5–4.5(–5.5) mm.; filaments 3–5.5 mm. long, with 2 spurs to ca. 0.5 mm. long. Capsule subglobose to globose or less commonly short-ovoid, 2.5–4.5 by 3–4.5 mm., with 5 pale, quite thickened sutures that in dehiscence remain attached to an adjacent valve. (FIGURE 21; see also Okuyama (1959) and Makino (1961) for drawings based upon Japanese material, and Matsumura (1916), Kanehira (1936), Liu (1962), and Li (1963) for drawings from Taiwanese material.)

DISTRIBUTION. Japan (chiefly western and southern Honshu, Kyushu, and Shikoku) and Taiwan (MAP 6; see also Horikawa, 1975).

ECOLOGY. Temperate to warm-temperate regions; *Tsuga sieboldii*–*Cleyera*

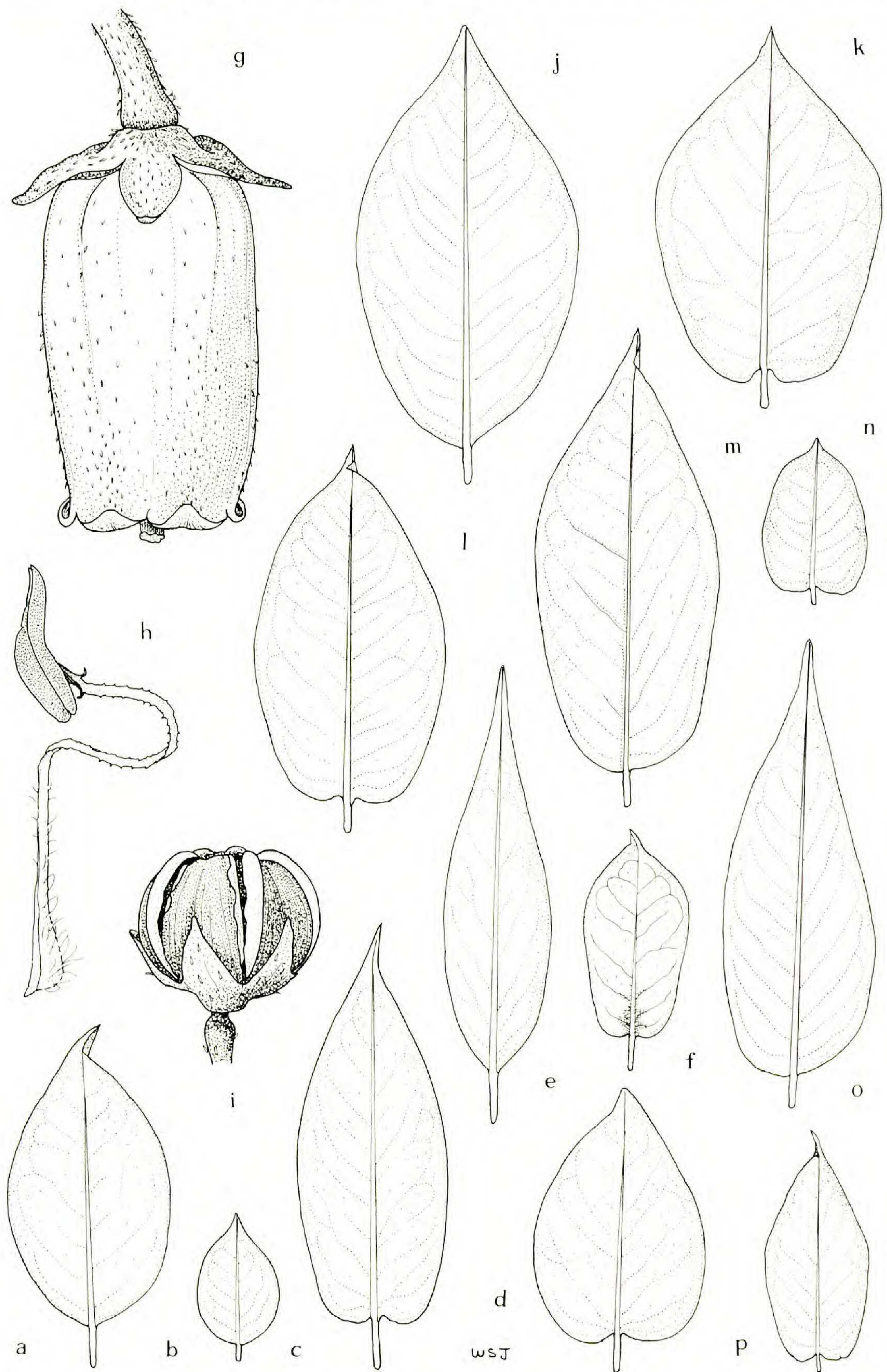
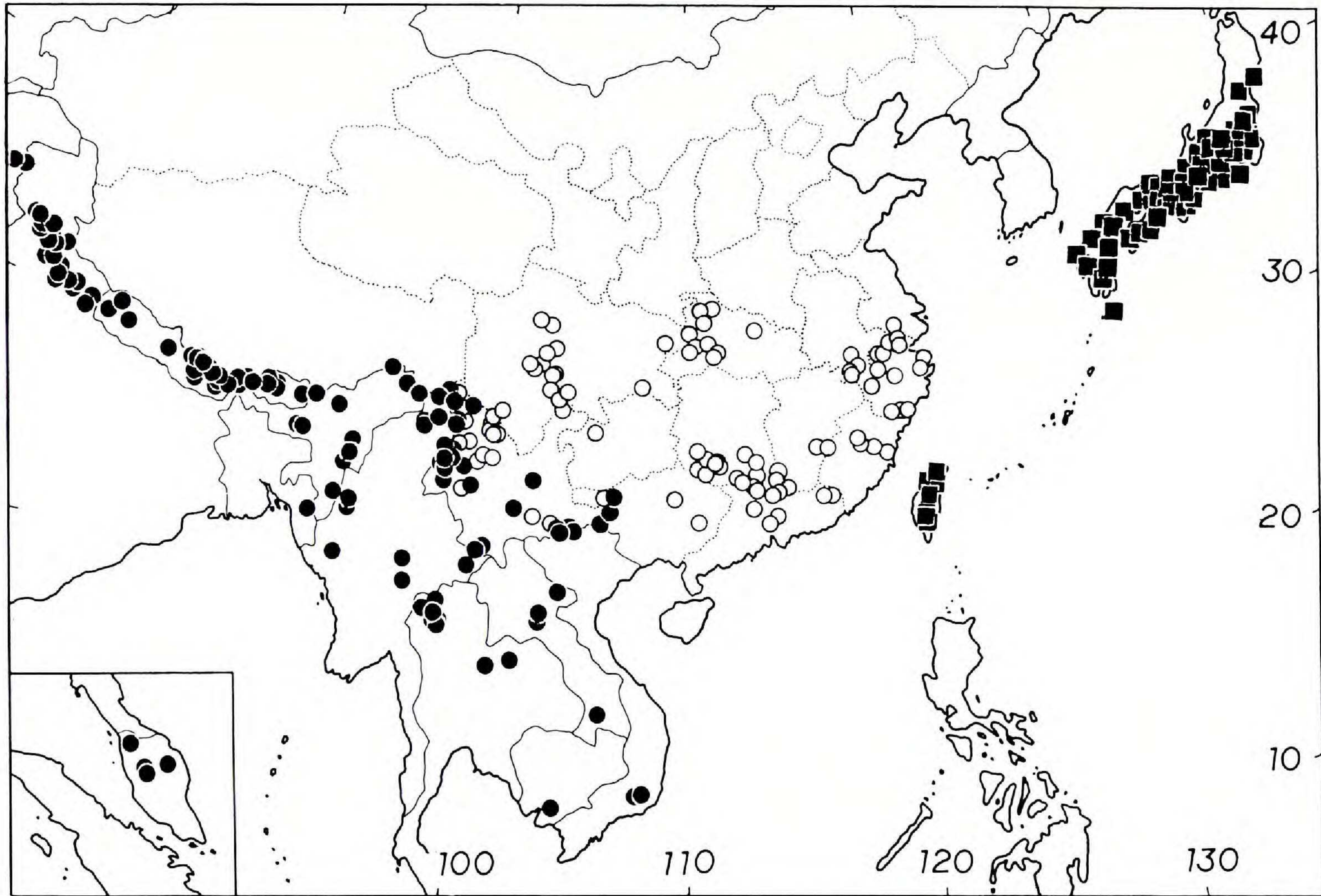


FIGURE 21. a-i, *Lyonia ovalifolia* var. *elliptica*: a-f, leaves, $\times .5$ (in f note tuft of long unicellular hairs on abaxial surface); g, flower, $\times 6$; h, stamen, $\times 12.5$; i, capsule, $\times 6$. j-p, *L. ovalifolia* var. *hebecarpa*, leaves, $\times .5$.



MAP 6. Distribution of *Lyonia ovalifolia* var. *elliptica* (squares), *L. ovalifolia* var. *hebecarpa* (circles), and *L. ovalifolia* var. *ovalifolia* (dots).

japonica-*Symplocos myrtacea* forests, *Castanopsis cuspidata*-*Cleyera japonica* forests, *Castanopsis cuspidata*-*Rapanaea neriifolia* forests, *Tsuga sieboldii*-*Pseudotsuga japonica* forests, *Fagus crenata* forests, thickets, mountain ridges, grasslands, dry sunny slopes, forest margins, and near hot springs; 1800-2700 m. alt. See Tatewaki & Misumi (1957) and Yatoh (1960) for characteristic species of the above-mentioned forest types. In Japan flowering chiefly late May through July (varying with elevation, latitude, season); on Taiwan as early as April in some areas, extending through July.

COMMON NAMES. Nejiki or neziki (Japan); seiban-nejiki or Taiwan-nejiki (Taiwan).

REPRESENTATIVE SPECIMENS. **Taiwan:** Yang-min-shan, Taipei Hsien, *Chen s.n.*, 28 March 1959 (TAI); Ari-san, *Faurie 172* (A); near sulfur hot springs, Taipeh, *Faurie 294* (P, UC, W); Chu-shan, Chiayi Hsien, *Hsu & Chuma 8928* (TAI); Mt. Ho-huan to Mt. Lee-shan, Tai-chung Hsien, *Huang 4679* (TAI); Mt. Stone, Kao-hsiung, *Huang 6510* (TAI); Ta-pa-chien-shan, Hsin-chu Hsien, *Kouh 3817* (TAI); Mt. Housha-shan, Hwaling, *Liu & Liu 180* (TAI); Mt. A-li, Ohia-yi Hsien, *Liu 337* (A); Mt. Nanhuta-shan, Ilan Hsien, *Tamura & Shimizu 20599* (E, S); Sozan, Taihoku Hsien, *Wilson 10771* (A, K, US); Ari-san to Mt. Morrison, *Wilson 10942* (A, US); Tsuei-fung to Sung-kang, Nantou Hsien, *Wu, Leu, & Chiu 7706* (TAI). **Japan.** CENTRAL HONSHU: Aichi pref., Mt. Hooraiji, Minamishidara-gun, *Kanai 6870* (A, TAI, TI); Awaji prov., Sumoto Is., *Murai 3024* (A); Echigo prov., Niigata-ken, Mt. Komagatake, *Nakamura s.n.*, 31 Aug. 1905 (TNS); Echizen prov., Itoo-mura, *Maeda 10466* (A); Fukui pref., Tsuruga-city, Yamanaka, *Hasegawa s.n.*, 30 June 1968 (TI); Gifu pref., Do, Sakashita-mura, Yoshiki-gun, *Kanai 6309* (TAI); Gumma prov., Nishikurozawa, Mt. Tanikawa, *Suzuki 69* (A); Hida prov., *Tomioke 5976* (A); Hitachi prov., Mt. Tsukuba, *Kobayashi 3020* (A, S); Hyogo pref., Mt. Rokko, *Hiroe 14067* (UC); Ise prov., Mie-ken, Takami Pass, *Sakurai s.n.*, May 1888 (TNS); Kai prov., Yamanashi-ken, Mt. Mitsutoge, *Hiyama 5149* (KAI, TNS); Kyoto pref., Mt. Arashiyama, W. of Kyoto-city, *Hiroe 13972* (UC); Mikawa prov., Tsugeno, *Kitamura s.n.*, 26 July 1952 (A); Mino prov., *Ito 7916* (A); Musashi prov., Kori-mura, Nishitama-gun, *Mizushima 2324* (A); Nagano pref., Hara-mura, Suwa-gun, *Kanai 6311* (A, TI); Nara pref., Mt. Omine, Yoshino-gun, *Shimizu 4375* (S); Osaka pref., Tannowa, *Muroi 6753* (A); Owari prov., *Kato 8776* (A); Settsu prov., Yamamoto, *Togasi T.N.S. 1503* (A, K, MAK, TNS, UC, W); Shiga pref., Mt. Uchimi, Shiga-gun, *Kitamura & Murata 2371* (MAK); Shimotsuke prov., Jakkotaki trail, Nikko, *Mizushima 2282* (A); Shinano prov., Narai, *Jack s.n.*, 3 Sept. 1905 (A); Tochigi pref., Kuroiso-cho, *Ide s.n.*, 16 June 1940 (TNS); Tokyo pref., Murayama reservoir, *Kanai 6310* (TAI); Totomi prov., Aratama-mura, Inasa-gun, Shizuoka pref., *Furuse s.n.*, 11 Oct. 1960 (S); Yamashiro prov., Mt. Daimonji, *Kitamura s.n.*, 20 Sept. 1936 (A). NORTHERN HONSHU: Fukushima pref., Omotego-mura, Nishishirakawa-gun, *Makino Herb. 81385* (MAK); Rikuzen prov., Akiu, *Ohashi 3053* (TI); Uzen prov., Yamagata-ken, Yonezawa, *Matsushima T.N.S. 37101* (TNS). WESTERN HONSHU: Bizen prov., *Masamune s.n.*, 7 Oct. 1925 (NY); Okayama pref., Mituisi, *Muroi 4810* (A); Suo prov., Mt. Gabi, Murozumi, *Migo s.n.*, 13 July 1954 (A); Yamaguchi pref., 2.5 mi. SW. of Yokoyama, Iwahuni-city, *Charette 1723* (S, UC). KYUSHU: Bungo prov., Beppu, *Ishidoya s.n.*, Aug. 1917 (A); Fukuoka pref., Hakozaki, near Fukuyoka-city, *Ichikawa 22* (A, W); Hizen prov., Nagasaki, *Faurie 3441*

(P); Miyazaki pref., Obi, *Hattori s.n.*, 26 May 1948 (s); Osumi prov., Mt. Takakuma, *Kawagoe s.n.*, 9 Nov. 1917 (A); Tanegashima Is., *Yano s.n.*, 31 July 1964 (MAK). SHIKOKU: Iyo prov., Hiroshima, *Togashi s.n.*, 11 May 1961 (TI); Tokushima pref., Mt. Otaki, Mima-gun, *Makino Herb. 105379* (MAK); Tosa prov., Takeyashiki, *Watanabe s.n.*, 13 June 1887 (UC).

3b. *Lyonia ovalifolia* (Wallich) Drude var. *hebecarpa* (Franchet ex Forbes & Hemsley) Chun, *Sunyatsenia* 4: 253. 1940.

Pieris ovalifolia (Wallich) D. Don var. *hebecarpa* Franchet ex Forbes & Hemsley, *Jour. Linn. Soc. Bot.* 26: 17. 1889. *Xolisma ovalifolia* (Wallich) Rehder var. *hebecarpa* (Franchet ex Forbes & Hemsley) Metcalf, *Jour. Arnold Arb.* 12: 275. 1931. TYPE: China, prov. Chekiang, Meichi, *Poli s.n.* (not seen).

Pieris henryi Lévl. *Bull. Soc. Bot. France* 53: 204. 1906. TYPE: China, prov. Yunnan, Mengtze, mountains, 6500 ft. alt., *A. Henry 9681* (holotype, E!; fragment of holotype, A!).

Pieris mairei Lévl. *Bull. Acad. Int. Géogr. Bot.* 25: 21. 1915. TYPE: China, prov. Yunnan, collines calcaires de Tcha-Ho, 2600 m. alt., July 1912, *E. E. Maire s.n.* (holotype, E!; fragment of holotype, A!; isotype, E!).

Pieris mairei Lévl. var. *parvifolia* Lévl. *Bull. Acad. Int. Géogr. Bot.* 25: 21. 1915. TYPE: China, prov. Yunnan, collines arides de Tche-Hai, 2500 m. alt., June 1912, *E. E. Maire s.n.* (holotype, E!; fragment of holotype, A!).

Deciduous shrub to moderate-sized tree to 5(-15) meters tall. Buds 1-11.5 by 1-4.5 mm. Leaf blades ovate, obovate, or elliptic, 5-12.5(-15) by 2.3-6(-8) cm., mesophyll unligified; apex acuminate to long-acuminate, often folded over in pressing; base rounded to cordate; venation brochidodromous, 2° veins sinuous or irregular; abaxial surface not papillose, glaucous or green, glabrous or sparsely pubescent along proximal portion of midvein, never with dense tuft of long-unicellular hairs at leaf base; petiole 3-14 mm. long. Inflorescences (2.5-)3.5-13(-16) cm. long, usually with 1 to 4 large, leaflike bracts to 2.5-6(-9) cm. long near base. Calyx lobes 1-2.5(-3) by 0.6-1.5 mm.; corolla cylindrical, 6.5-11.5 by 2.5-6.5 mm.; filaments 4-6.5 mm. long, with 2 spurs to ca. 0.5 mm. long. Capsule globose to subglobose or short-ovoid, 2.5-4 by 2.5-4 mm., with 5 pale, thickened sutures that in dehiscence remain attached to an adjacent valve. (FIGURE 21; see also Fang, 1944, labeled as *Lyonia ovalifolia* var. *elliptica*, and Anonymous, 1974a.)

DISTRIBUTION. China, Kiangsu and Anhwei west to Szechwan and Yunnan, south to Kwangsi and Kwangtung (MAP 6).

ECOLOGY. Both cold- and warm-temperate areas; open pine and oak forests, forest margins, thickets, meadows, dry and/or rocky slopes, often along streams; ca. 120-3300(-3800) m. alt. in Yunnan and Szechwan provinces, 2300 m. or less elsewhere. Flowering May through early August, usually peaking June or July.

REPRESENTATIVE SPECIMENS. **China.** KIANGSU: I-Hsing, Lungche Mt., *Keng 2460* (A). ANHWEI: Wang-che, S. Chu-hwa shan, *Ching 2838* (A, E, K, UC); Wu

Yuen, *Ling* 1315 (UC); Wang Shan, above Tiao Ch'tao, *Steward* 1250 (A, E, UC). CHEKIANG: Mogan Shan, *Cheo & Wilson* 42 (GH, UC); Sze-ton, S. of Siachu, *Ching* 1693 (A, UC, W); W. of Wenchow, *Ching* 1843 (A, E, GH, UC, US); Ping Ying, toward Tai Suan, *Ching* 2094 (A, K, US, W); Tein-mu Shan, *Ching* 6184 (A, E, UC); Chun-an Hsien, *Keng* 675 (A, UC); Chang-shan Hsien, *Keng* 832 (A, UC); Tung-yang Hsien, *Keng* 934 (A, UC); Mei-chi, An-chi Hsien, *Liu & Ching* 4928 (A, E, K, UC); near Ningpo, *Macgregor s.n.*, 1908 (A); Han-chow, *Meyer* 396 (A). Kiangsi: Shui-shueng Hsien, *Hsiung* 5525 (A); Ta Yu Hsien, *Hu* 970 (A); Ningdu near Yuanhsiang-schi, *Hui* 360 (A, E, W); Kiennan distr., Sai Hang Cheung, *Lau* 4321 (A, S, US); Lungnan distr., Oo Chi Shan, *Lau* 4403 (A, S, US). FUKIEN: Yenping, Chi-yuan-keng bat cave, *Chung* 2980 (A, E, K, UC, W); Kuliang, *Chung* 6618 (A, F); Kutien, *Chung's coll.* 4034 (A). KWANGTUNG: Canton, *Carles s.n.*, March 1877 (E); NW. Kwangtung near Hunan border, Gantung, *Fenzel* 71 (UC); S. of Mei Hsien, Tsin Leong San, *Gressitt* 1237 (A, E, UC); Yu-yuen, *Ko* 52711 (A); Wung Yuen distr., Tsing Wan Shan, *Lau* 2073 (A); Luang-lin, Ta-pu, *Schindler* 437c (K); Lung T'au Mt., near Iu, *To & Tsang* 361, C.C.C. 12360 (E, S, UC, W); Sam Kok Shan, Tsungfa and Lungmoon, *Tsang* 20541 (US, W); Yao Shan, Lokchong, *Tso* 20766 (E); Ying-tak distr., *Wang* 549 (A, W). HUPEH: Tzu-kwei Hsien, *Chow* 373 (A, E); Huan Tsan, *Chun* 4104 (A); Chien-shih, *Henry* 5806a (A, E, GH, K, US); Ou-tan-scian, *Silvestri* 3127 (A); I-chang, *Wilson* 492 (A, E, GH, W); Chang-yang Hsien, *Wilson* 3189 (A, E, GH, K, W); Fang Hsien, *Wilson* 3188 (A, E, GH, W); Patung Hsien, *Wilson* 492a (A). HUNAN: Tienchaosan, *Dahlstrom* 272 (S); Yang Shan, Changning Hsien, *Fan & Li* 203 (A, L, W); Sinning Hsien, Ma-Ling-Tung, *Fan & Li* 455 (A, L, W); near Wukang, *Handel-Mazzetti* 11995 (A, E, W). KWEICHOW: Ku-kai Shan, Tating, *Tsiang* 8836 (E, S, UC). KWANGSI: Bin Long, Min Shan, N. Luchen, *Ching* 6040 (A, W); Shing-An Hsien, Ssn-Men-Chien, Tu-Ti-Tang, *Chung* 81803 (A); Tzu Yuen distr., *Chung* 83519 (A); Pai-yun-an, Ch'uan distr., *Tsang* 27225 (A); Ling-ch'uan distr., Ta-ling, *Tsang* 27895 (A, UC). SZECHWAN: Omei Shan, *Chiao & Fan* 163 (A); Po-shin Hsien, *Chu* 2975 (A, E, K); Po-shin, *Chu* 3669 (A, E); Chin-fu Shan, Nan-chuan Hsien, *Fang* 601 (A); Kuan Hsien, *Fang* 2095 (A, E); Luting Hsien, *Fang* 3229 (A, E); Wen-chuan Hsien, Tsao-puh, *Hu* 2301 (A); Wan Hsien, Mon-tao-chi, Shih-men-pa, *Hwa* 73 (A, UC); Mt. Tien-chuan, *Liu* 1336 (A); near Tachienlu, *Pratt* 279 (K, P); S. of Muli, *Rock* 16127 (A, E, US); Opien Hsien, *Sun* 943 (US); SE. of Mao Hsien, *Wang* 21975 (A); Wu-shan, *Wilson* 1157 (A, E, GH, W); Mo-pin, *Wilson* 3190 (A, E, W); Ping-shan Hsien, *Yü* 3111 (E); Lei-po Hsien, *Yü* 3346 (E). YUNNAN: W. Likiang, Ta-mi-chung, *Ching* 21588 (A); E. flank of Tali Range, 25°40'N., *Forrest* 4180 (A, E, K); hills forming E. boundary of Lichiang Valley, 27°25'N., *Forrest* 6112 (E); Lichiang Range, 27°40'N., *Forrest* 10172 (A, E, K); Mekong-Salwin divide, 27°54'N., 98°50'E., *Forrest* 19647 (A, E, K, UC, W); ranges S. of Yung-chang-fu Valley, 24°50'N., 99°20'E., *Forrest* 24349 (E, K); Tché-hai, *Maire* (A); Tsekou, *Soulier* 1376 (F); Yung-shan Hsien, *Tsai* 51118 (A); Pin-chuan Hsien, *Tsai* 52976 (A); Shih-ping Hsien to Ping Shan, *Tsai* 53352 (E); Ta-li Hsien, *Tsai* 53826a (A, E); Lan-ping Hsien, *Tsai* 56268 (A); Wei-se Hsien, *Tsai* 57861 (A); Huan-fu-ping, *Wang* 69334 (A).

3c. *Lyonia ovalifolia* (Wallich) Drude var. *doyonensis* (Hand.-Mazz.) Judd, comb. et stat. nov.

Pieris doyonensis Hand.-Mazz. Anzeig. Akad. Wiss. Wien Math.-Naturwiss. Kl. **60**: 185. 1923. *Lyonia doyonensis* (Hand.-Mazz.) Hand.-Mazz. Symb. Sin. **7**: 789. 1936. TYPE: China, prov. Yunnan, Doyon-lumba Valley near Lu-djiang (Salween), 28°2'N., 2700–2900 m. alt., *Handel-Mazzetti* 9600 (holotype, w!; fragment of holotype, A!; isotypes, A!, E!).

More or less deciduous shrub to moderate-sized tree to 5(–12) meters tall. Buds 1–11 by 1–7 mm. Leaf blades nearly orbicular to widely obovate or ovate, (4–)6–12(–16) by 5.3–10(–12) cm.; mesophyll unligified; apex usually truncately short-acuminate; base rounded to cordate; venation ± brochidodromous, 2° veins smoothly arching toward margin to slightly irregular or sinuous; abaxial surface obscurely to clearly papillose, glaucous or green, glabrous; petiole 7–15 mm. long. Inflorescences (5–)6–12(–20) cm. long, usually with ca. 1 to 3 large, leaflike bracts to 3–7.5 cm. long near base. Calyx lobes 1.7–2.7 by 0.9–1.8 mm.; corolla cylindrical, 9–13 by 3.5–6.5 mm.; filaments 4–7 mm. long, with 2 spurs to ca. 0.4 mm. long. Capsule ± subglobose, 3–3.5 by 3.5–5 mm., with 5 pale, quite thickened sutures that in dehiscence usually remain attached to an adjacent valve. (FIGURE 22; see also Anonymous, 1974a.)

DISTRIBUTION AND ECOLOGY. Northwestern Yunnan (China) and adjacent areas of northern Burma and extreme southeastern Tibet (MAP 5). Pine forest, open woods, wooded ravines and slopes, thickets, along river banks; ca. (2000–)2400–3350 m. alt. Flowering chiefly June through early August.

REPRESENTATIVE SPECIMENS. **China**. YUNNAN: Wei Hsi, *McLaren's collectors* D177 (A, E); Chih-tse-lo, *Tsai* 54118 (A, PE); Shang-pa Hsien, *Tsai* 54456 (A, PE); Upper Kiukiang Valley, (Clulung) Bang, *Yü* 19552 (A, E). TIBET: Tsarong, Salwin–Kui Chiang Divide, 28°75'N., *Forrest* 19860 (A, E, K); Laktang, *Ward* 3459 (E). **Burma**: flank of N'Mai-kha–Salwin Divide, 26°20'N., *Forrest* 29654 (E); Adung Valley, 28°20'N., 97°45'E., *Ward* 9572 (A).

3d. *Lyonia ovalifolia* (Wallich) Drude var. *ovalifolia*

Andromeda ovalifolia Wallich, Asiatic Res. **12**: 391. 1820. *Andromeda capricida* Ham. ex D. Don, *pro. syn.*, Prodr. Fl. Nepal. 149. 1825. *Pieris ovalifolia* (Wallich) D. Don, Edinb. New Philos. Jour. **17**: 159. 1834. *Xolisma ovalifolia* (Wallich) Rehder, Jour. Arnold Arb. **5**: 52. 1924. TYPE: Nepal, without definite locality, *Wallich s.n.*, May 1818 (holotype, BM?, not seen; presumed isotypes, A!, UC!).

Andromeda ovalifolia var. *cordata* Govan ex Wallich, Catal. Indian Pl. no. 763B. 1829. TYPE: [India, Uttar Pradesh], E. Saharanpur, *Wallich s.n.*, 16 April [?—nearly illegible] (lectotype, K-w (IDC 7394. 90: II. 4!)). This name was first published as either a species or a variety by Wallich (1820). Since a rank was not designated, the name was not validly published until 1829, when Wallich listed it as a variety of *Lyonia ovalifolia*.

Deciduous to semi-evergreen shrub to moderate-sized tree to 7.5(–18) meters tall. Buds 1–11.5 by 1–6.5 mm. Leaf blades ovate or elliptic to slightly obovate, (4–)6–15(–21) by (2–)3.5–8.5(–11.5) cm.; mesophyll unligified; apex acuminate;

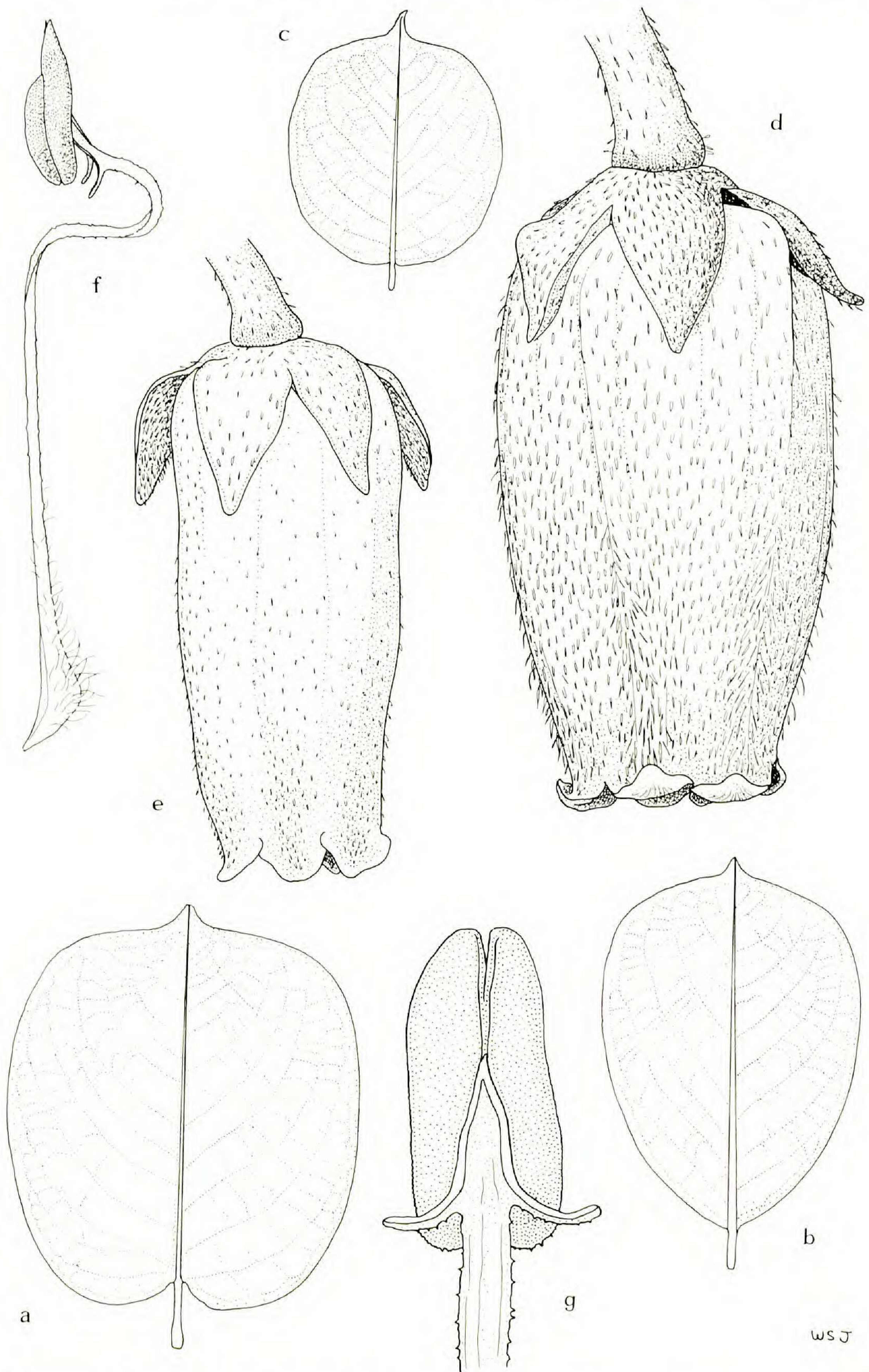


FIGURE 22. a-d, *Lyonia ovalifolia* var. *doyonensis*: a-c, leaves, $\times .5$; d, flower, $\times 6$. e-g, *L. ovalifolia* var. *ovalifolia* (in part): e, flower, characteristic of populations of western India, $\times 6$; f, stamen, $\times 12.5$; g, anther, $\times 25$.

base rounded to cordate, or widely cuneate; venation eucamptodromous to slightly brochidodromous toward apex, 2° veins usually smoothly arching toward margin; abaxial surface sometimes papillose and/or glaucous, usually not shiny yellowish- to gold-green, and glabrous or sparsely pubescent along proximal portion of midvein and occasionally also adjacent 2° veins; petiole 4–15(–20) mm. long. Inflorescences 3–16(–30) cm. long, usually with ca. 1 to 4 large, leaflike bracts to 2–8(–11.5) cm. long near base. Calyx lobes (1–)1.5–2.5(–4) by 0.8–1.5(–2) mm.; corolla cylindrical, (7–)8–12(–13.5) by 2.5–5(–7) mm.; filaments 5–9 mm. long, with 2 spurs to ca. 0.5 mm. long. Capsule usually subglobose to globose, 2.5–4.5 by 3.5–6 mm., with 5 pale, quite to sometimes only slightly thickened sutures that in dehiscence remain attached to an adjacent valve. (FIGURES 22, 23; see also Wallich (1820), Wight (1850), Sleumer (1967), Anonymous (1974a), and Hara (1968).)

DISTRIBUTION. China, western Kwangsi and Yunnan, south to Thailand and Malay Peninsula, west along Himalayas to northwestern India and Pakistan (MAP 6).

ECOLOGY. Cool- to warm-temperate areas; recorded from *Schima-Castanopsis* forests; various *Pinus* forests; rocky and rather dry slopes with oaks and/or pines; various *Quercus* forests; *Quercus-Vaccinium* thickets; *Quercus* spp.-*Keteleeria rouletii* forests, dry forests of *Quercus* spp. and *Rhododendron arboreum*; *Rhododendron* thickets; savannas with *Craibiodendron*; warm- to cool-temperate mixed broadleaved forests; dwarf, lichen-laden cloud forests; *Picea-Pinus* forests; *Tsuga dumosa* forests; *Abies spectabilis* forests (low portions); along streams, swamp, and forest margins; disturbed and/or burned areas; open sandstone savannas; ca. (700–)850–3050 m. alt. For more detailed discussions of the above-listed forest types, see Ohashi (1975), Stainton (1972), Malla *et al.* (1973), Suwal (1969), Schweinfurth (1957), and Hara (1966) for Nepal; Osmaston (1927), Parker (1924), Kanjilal *et al.* (1939) for India; Kingdon-Ward (1941, 1944, 1945) for Burma; Vidal (1960) for Laos; and Wang (1939) for Yunnan. Open, sunny areas favored; quite resistant to fires and often found in periodically burnt areas. Grows in cut-over and disturbed areas because of its sun-loving qualities and capability to spread vegetatively by underground rhizome network. Flowering chiefly (March to) April to July (to August), but varies greatly with elevation, latitude, and habitat.

COMMON NAMES. Muead-ngua (Thailand); nman-hpun (Jingpaw vern., northern Burma); anjīr, angiār (Brandis & Stewart, 1874), sagechu, sheabogi (Wallich, 1820), angri (Malla *et al.*, 1973) (Nepal); diengla samiang, jarahap (Khasi, Assam—Kanjilal *et al.*, 1939), ayār (Almora), aiaar, airee (Wallich, 1820), ailam (Kangra—Parker, 1924; Brandis, 1911), erau, yerta, yarta, ladrang, (Bashahr—Parker, 1924; Brandis, 1911), allain, ayatta, eilan, ellan, ellal, arur, rattankāt (Punjab—Brandis & Stewart, 1874; Brandis, 1911) (India); eyār, ayār (northwest frontier province, Brandis & Stewart, 1874), ratankāth (Hazara—Parker, 1924) (Pakistan).

REPRESENTATIVE SPECIMENS. **China.** KWANGSI: Bako Shan, W. Poseh, *Ching* 7470 (A, E); Chen Pien distr., *Ko* 55845 (A); Ling-yun Hsien, *Steward & Cheo*

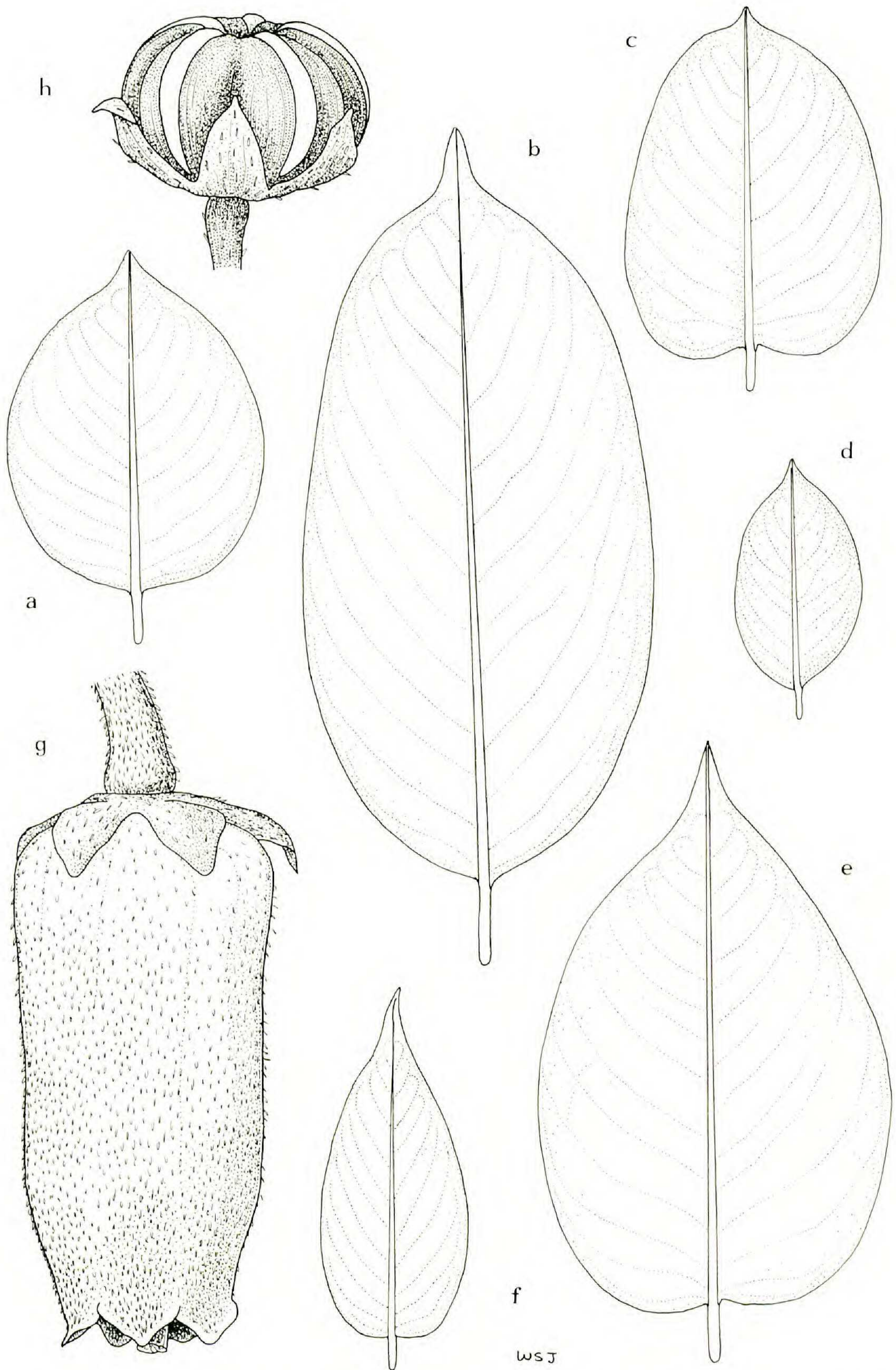


FIGURE 23. *Lyonia ovalifolia* var. *ovalifolia* (in part): a-f, leaves, $\times .5$; g, flower, characteristic of Yunnan populations, $\times 6$; h, capsule, $\times 6$.

660 (A, S, W). YUNNAN: Yunnan-sen distr., *Cavalerie* 4574 (E, K); Fo-Hai, *Fang* 73855 (TAI); S. Chungtein, Ta-li, on Yangtze bank, *Fang* 3212 (A); Wen-shan Hsien, *Fang* 11065 (A); Mar-li-po, Chung-dzia, *Fang* 12716 (A); Salween valley, near Lu-chang, 26°N., *Forrest* 1107 (E); N'Maikha region, *Forrest* 1820 (E); banks of Shweli, 25°N., *Forrest* 7915 (E); W. flank of Shweli-Salween divide, 25°20'N., *Forrest* 14633 (A, K, W); N'Maikha-Salwin divide, 26°20'N., *Forrest* 18345 (A, E); vicinity of T'eng-yueh, 25°N., 98°36'E., *Forrest* 24295 (E); W. of Lung-pan, 25°50'N., 98°33'E., *Forrest* 27743 (A, E); Mengtse, *Henry* 9091F (A, E, S); between T'eng-yueh and Lung-ling, *Rock* 7167 (A, UC, US); N. of Yunnan-fu, between Schi-lung-pa and Ta-sung-chu, *Schneider* 374 (A); Shang-pa, *Tsai* 54790 (A); Lung-ling Hsien, *Tsai* 55015 (A); Ping-pien Hsien, *Tsai* 60266 (A, E); W. of Champu-tung, Chiu-kiang, *Wang* 67037 (A); Nan-chiao, *Wang* 75258 (A); W. of Tung-hai, *Wissmann* 44 (W); Shunning, Hila, Wumulung, *Yü* 16655 (A, E); Kiukiang Valley, Lahpi to Tangtehwang, *Yü* 19939 (A, E); Salween-Kiukiang divide, Swangchiang, *Yü* 22086 (A, E). TIBET: Salween-Kui-chang divide, 28°40'N., 98°15'E., *Forrest* 19136 (A, E, K); prov. Monyul, Nyam Jang Chu, Lepo, 27°47'N., 91°50'E., *Ludlow et al.* 6453 (E); Shakti, Nyam Jang Chu, *Ludlow et al.* 12566 (E); Tsangpo Gorge, *Ward* 6373 (E, K); Tha Chu Valley, *Ward* 19666 (E). VIETNAM: Da-lat, *Hayata* 593 (A); Valley of Dong-nai, *Poilane* 9576 (P, US); E. of Dankia, Langbiang, *Poilane* 18698 (P). LAOS: Pu Bia, *Kerr* 21045 (E); Sam Neua, *Poilane* 2070 (A, B, K); Xing-huang, prov. Trammel, *Poilane* 2258 (A, B); Pakson, Boloven plateau, *Poilane* 28475 (L). CAMBODIA: M. de l'éléphant, *Poilane* 264 (A, K). THAILAND: S. side of Doi Suthep, Chiang Mai, 18°50'N., 97°54'E., *Abbe et al.* 9286 (A, E, K, L); Phukrading, Loey, 16°55'N., 101°47'E., *Abbe et al.* 9435 (A); Doi Pui, Chiang Mai, *van Beusekom & Phengkhlai* 1270 (E, K, L); Phu Miang, Loey, *Hansen et al.* 11147 (E, L); Doi Chong, 19°25'N., 98°18'E., *Hansen & Smitinand* 12640 (E, L, P); Doi Angka, *Kerr* 5321 (E); Me Tun, Chieng-mai, *Kerr* 6241 (UC); Doi Chieng-dao, Payap, *Put* 4492 (E). MALAYSIA: Perak, W. crest of Brinchang, 4°31'N., 101°17'E., *Abbe et al.* 9754 (A, E, K, L); Kedah, Gunong Jerai, *Dolman KEP* 20745 (K); Pahang, Gunong Baku Brinahang, *Henderson SFN* 23594 (A); Pahang, Gunong Tahan, *Holttum SFN* 31384 (A); Kedah, Kedah Peak, *Symington KFN* 46848 (L); Cameron Highlands, Robinson Falls near Tanah Rata, *Sleumer* 4662 (L). BURMA: Mt. Victoria [Pakokku Hill Tracts], *Cooper* 6006 (E, UC); Haka, *Dickason* 7391 (A, E, L); Wunba Taung, Chin Hills, *Dickason* 8461 (A, E, L); Lawksawk state, Ah Shai Myin, *Dickason* 8716 (A, E, L); N'Maikha-Salween Divide, 26°00'N., *Forrest* 29731 (E); Fort Stedman, *Huk s.n.*, Jan. 1893 (E, W); Kachin state, Sumprabum sub.-div., between Tsuptaung and Kanang, *Keenan et al.* 3421 (A, E, K); Kanat Bum, *Keenan et al.* 3455 (A, E, K); SE. Shan states, Keng Tung territory, Meh Lui valley, *Rock* 2315 (A, UC, W); Kahao, Zayul R., *Ward* 7154 (K); N. Triangle, Kachin state, *Ward* 21200 (A, E). BHUTAN: Chepcha Dimpu, *Cooper* 1313 (E); Gichha Punakha, *Cooper* 2761 (E); Tilagong Punakha, *Cooper* 2821 (E); Samtengang, Tashi Choling, *Hara et al.* 1118 (TI); Balfai, near Trashigong, *Ludlow & Sherriff* 571 (E); Kyi La, Mangde Chu Valley, *Ludlow & Sherriff* 3013 (E); Gyasa Dzong, Mo Chu, *Ludlow et al.* 16526 (A, E); Tobran, Trashiyangse Chu, *Ludlow et al.* 20490 (E). NEPAL: Godawari, *Bhatt* 330 (UC); above Dhunche, Gosainkund, *Hara et al.* 69967 (TI); Dhankuta, *Hara et al.* 6304475 (A, TI); Ghatte-khebang, *Hara et al.* 6304482 (TI); Kakani, Kathmandu, *Kanai* 674987 (TI); Trisuli Valley, Syabrubensi, *Lyon* 31 (E); between Grang and Thare, E. side of Trisuli R., *Nicolson* 2364 (US); Sindhu Palchok distr., below Helumbu, *Nicolson* 2659 (US); Lekh Rangchi,

Polunin et al. 527 (E); Darma Tarke Khola, *Polunin et al.* 4338 (A, E); Ranga Chauthaka, S. of Chakure Lekh, *Polunin et al.* 5550 (A, E); Langtang Valley, *Schilling* 497 (K); Arun Valley, Kandbari, E. of Dingla, *Stainton* 102 (E); Tarakhola, W. of Beni, *Stainton et al.* 165 (E); Arun Valley, Sedua, NW. of Num, *Stainton* 677 (A, E); near Lumsum, *Stainton et al.* 2566 (A, E); upper Buni Gandaki, 28°32'N., 84°90'E., *Stainton* 3918 (E); Bhujung, NE. Chanpokhara, *Stainton et al.* 5114 (E). **Bangladesh:** Chittagong div., *Cowan* 1016 (E). **India.** ARUNACHAL PRADESH: W. corner of Apa tani Valley, Subansiri div., *Cox & Hutchinson* 527 (E); Delei Valley, 28°20'N., 96°35'E., *Ward* 8480 (K); Kahao, *Ward* 19491 (E). NAGALAND: Naga Hills, Kohima, *Prain s.n.*, June 1886 (E, L, W). MANIPUR: Muku, *Watt* 5074 (E); Metaiphum, *Watt* 6075 (E); Khongui Valley, *Watt* 6766 (E). MIZORAM: Lushai Hills, Chakang, *Parry* 109 (L). MEGHALAYA: Mamlu, *Bar* 20931 (L); near Upper Shillong, Khasia Hills, *Cox & Hutchinson* 544 (E, K); Shillong Peak, *Rao* 2766 (L); Khasia and Jaintia Hills, Umran, *Ruse* 19 (A). SIKKIM: Pamianchi, Tingling Bridge, *Hara et al.* 5319 (A, TI); Phalut-Dentam, *Hara et al.* 5320 (A, TI); Lachen, *J. D. Hooker s.n.*, May 17 (K); Zenni Valley, *Smith & Cave* 2718 (M, UC). WEST BENGAL: Darjeeling, *Lace* 2300 (E); Darjeeling, Happy Valley, *Hara et al.* 5322 (TI). UTTAR PRADESH: Naini Tal, Kumaon, *Brandis* 1667 (M); Kumaon, forest near Shankola, *Duthie* 3129 (K); Dehra Dun distr., vicinity of Musoorie, Woodstock, *Fleming* 460 (A); Jehu Garhwal, *Gamble s.n.*, 1 April 1898 (K); Garhwal, Batanbasa, Adnalarange, *Inayat* 25913 (K); Jaunsar, Kachanu, *Nand* 171 (E); Siwalik and Jaunsar div., Chakrata, *Rai* 30 (US); Garhwal, Gohrna-Ramni, *Rau* 10111 (A). HIMACHAL PRADESH: Simla prov., Mahasu, *Brandis* 1419 (A); Dalash-Chazahi, Kulu-Lahaul, *Drummond s.n.*, 19 May 1888 (E, K, UC); Simla, below Naldehoa, *Gamble* 6018 (K); Kulu Valley, *Jain & Bharadwaja s.n.*, 13 June 1950 (A); Kangra, Baijnath, *Koelz* 4538 (A, F, US); Kulu, Kakinal, *Koelz* 8339 (A, UC); Chamba state, Bara, *Lace* 735 (E); Bashahr state, Simla distr., Sarhan, *Parker* 2984 (A); Chamba state, Almi, Belj Valley, *Parker s.n.*, 23 June 1919 (A); Kulu, Parhratti Valley, *Parkinson* 3913 (E); Dharamsala, Kotwali Bazaar, *Stewart* 1875 (A, S). **Pakistan:** Hazara distr., Siran Valley, *Ianyat* 19902 (K); Azad Kashmir, Serimang, Punch, *Stewart & Nasir* 25498 (F, GH, W).

3e. *Lyonia ovalifolia* (Wallich) Drude var. *lanceolata* (Wallich) Hand.-Mazz.
Symb. Sin. 7: 788. 1936.

Andromeda lanceolata Wallich, Asiatic Res. 13: 390. 1820. *Andromeda squamulosa* D. Don, Prodr. Fl. Nepal. 149. 1825. *Pieris lanceolata* (Wallich) D. Don, Edinb. New Philos. Jour. 17: 159. 1834. *Pieris ovalifolia* (Wallich) D. Don. var. *lanceolata* (Wallich) Clarke in J. D. Hooker, Fl. Brit. India 3: 461. 1882. *Xolisma ovalifolia* (Wallich) Rehder var. *lanceolata* (Wallich) Rehder, Jour. Arnold Arb. 5: 52. 1924. TYPE: India, "in montosis Bengalae orientalis" [probably from Khasia Hills region] (not seen, but illustration in Wallich (1820) falls within variation pattern expressed by this taxon.)

Pieris kouyangensis Lévl. Bull. Acad. Int. Géogr. Bot. 12: 253. 1903. TYPE: China, Kouy-Tchéou [prov. Kweichow], vicinity of Kouyyang [Kueiyang], sur les montagnes du Collège, 18 May 1898, *Bodinier* 2264 (holotype, E!; fragment of holotype, A!; isotype, P!).

Pieris ulbrichii Lévl. Bull. Soc. Bot. France 53: 205. 1906. TYPE: China, Kouy-Tchéou [prov. Kweichow], without definite locality, 15 May 1904,

- Esquirol* 42 (holotype, E!; fragment of holotype, A!; isotype, E!).
- Vaccinium mairei* Lévl. Bull. Acad. Int. Géogr. Bot. **25**: 21. 1915. TYPE: China, prov. Yunnan, brousse des montagnes à Kigo-Me-Ti, 3200 m. alt., May 1912, *E. E. Maire s.n.* (holotype, E!; isotype, A!).
- Lyonia compta* (Smith & Jeffrey) Hand.-Mazz. var. *stenantha* Hand.-Mazz. Symb. Sin. **7**: 790. 1936. TYPE: China, prov. Yunnan, near Yunnanfu [Kun-ming], S. of Djindien-se Temple, 2100 m. alt., 23 May 1917, *Handel-Mazzetti 13077* (holotype, w!; isotypes, A!, E!).
- Pieris ovalifolia* (Wallich) D. Don var. *tomentosa* W. P. Fang, Contr. Biol. Lab. Chin. Assoc. Advancem. Sci. Sect. Bot. **10**: 241. 1938. TYPE: China, prov. Yunnan, Yung-jen-hsien, in ravines, 1700 m. alt., 24 May 1933, *Tsai 52887* (holotype, PE?, not seen; isotypes, A (2 sheets)!).

Deciduous to semi-evergreen shrub to small tree to 4(-10) meters tall. Buds 1-7.5 by 1-5.5 mm. Leaf blades elliptic or narrowly elliptic, to slightly ovate or obovate, 5-11(-14.5) by 2-4.8(-7) cm., mesophyll with at least partially developed layer of lignified cells near abaxial epidermis; apex acuminate; base narrowly cuneate to rounded; venation eucamptodromous to slightly brochidodromous toward apex, 2° veins usually smoothly arching toward margin; abaxial surface neither papillose nor glaucous, often shiny yellowish- or gold-green, glabrous or sparsely pubescent along proximal portion of midvein to rarely densely pubescent on all veins; petiole 5.5-14 mm. long. Inflorescences 2.5-9(-18) cm. long; usually with 1 to 5 large, leaflike bracts to 2-7(-11) cm. long near base. Calyx lobes (2-)2.5-4.5(-6.5) by 0.8-1.7(-2.5) mm.; corolla cylindrical, (7-)8-10(-12.5) by 3-5.5(-6.5) mm.; filaments 5-7.5 mm. long, with spurs to ca. 0.5 mm. long. Capsule short-ovoid or ovoid, to less commonly globose or subglobose, 3-5(-5.5) by 3-4.5(-5) mm., with 5 pale, quite thickened sutures that in dehiscence remain attached to an adjacent valve. (FIGURE 24; see also Wallich (1820), Wight (1850), Anonymous (1974a).)

DISTRIBUTION AND ECOLOGY. China, Yunnan and southern Szechwan, eastward into Kweichow and Kwangsi; disjunct populations in Kwangtung and Hainan, China, and Khasia Hills, India (MAP 7). *Pinus* and/or *Quercus* forests, *Castanopsis* forests, thickets, open areas with *Pteridium*, open woods, dry, rocky hillsides and ridges, gulleys, forest margins; ca. (365-)1100-2800(-3050) m. alt. Flowering chiefly (March to) April to early June.

REPRESENTATIVE SPECIMENS. **China.** KWANGTUNG: P'oon-Ue distr., White Cloud Mt., *McClure Y-121* (A); near Canton, Pakwan, *Sampson 16440* (K). HAINAN: Ch'ang-Kiang distr., Ka Chik Shan, *Lau 1608* (A). HUPEH: En-shih Hsien, *Chow 1856* (A, E). KWEICHOW: Tsingchen, Gou-R-Tan, *Teng 90289* (A); Pa-na, Chengfeng, *Tsiang 4293* (E, S, UC); Sa-chui, Tungtze, *Tsiang 4813* (E, M); Fan-ching-shan, Yinkiang, *Tsiang 7773* (E); Tui-po, Pi-chieh, *Tsiang 8976* (A, E). KWANGSI: Pin-lam, *Ko 55574* (A); Luchen, Pei Loo, Min Shan, *Ching 5946* (W); Ling-Yun Hsien, *Steward & Cheo 300* (A, S); SE. of Shang-sze, Shap Man Taai Shan, near Ping Hoh Village, *Tsang 22148* (A, S); Kwei-lin distr., San-min village, P'an-ku-shan and Ch'ao-t'ien-shan, *Tsang 27984* (UC); Yao Shan, Ping Nan, *Wang 39323* (A). SZECHWAN: Chung Hsien, *Fang 446* (A); Nanchuan Hsien, *Fang 1087* (A, E, K); Omei, *Fang 3331* (A, E); near

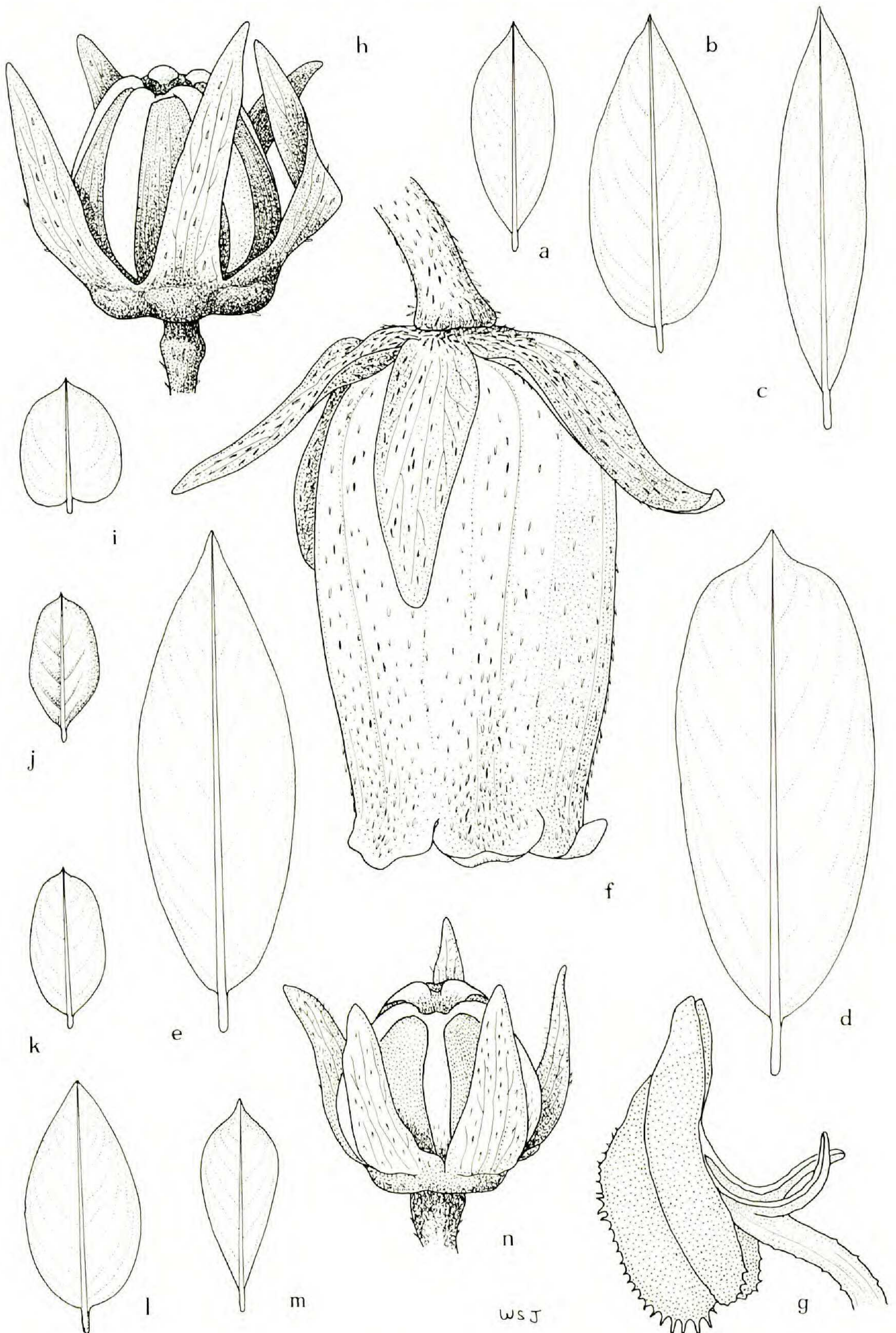
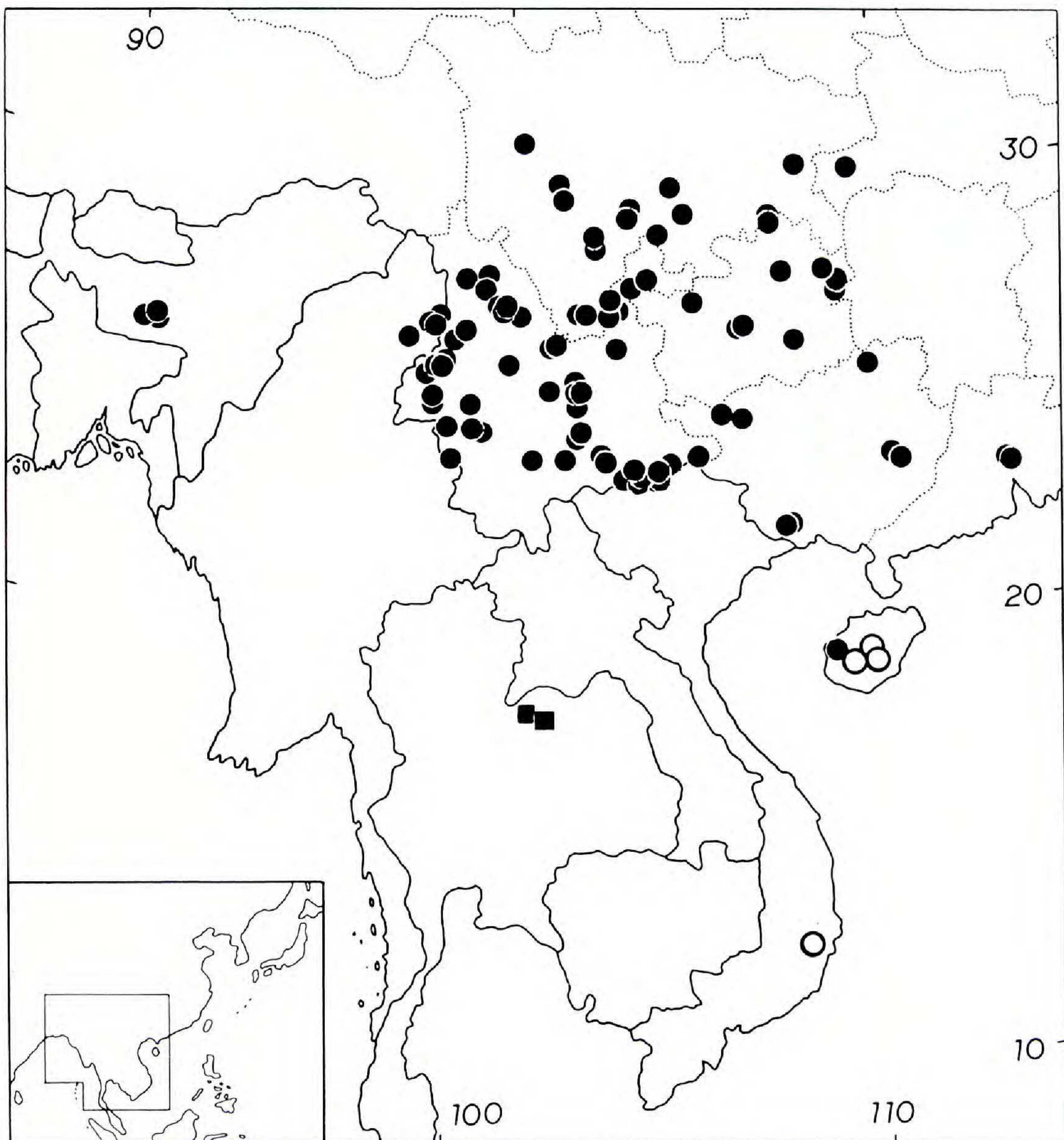


FIGURE 24. a-h, *Lyonia ovalifolia* var. *lanceolata*: a-e, leaves, $\times .5$; f, flower, $\times 6$; g, anther, $\times 25$; h, capsule, $\times 6$. i-n, *L. ovalifolia* var. *foliosa*: i-m, leaves, $\times .5$; n, capsule, $\times 6$.



MAP 7. Distribution of *Lyonia ovalifolia* var. *lanceolata* (dots), *L. ovalifolia* var. *rubrovenia* (circles), and *L. ovalifolia* var. *foliosa* (squares).

Ningyueh, *Handel-Mazzetti* 1778 (E, W); Ya-lung valley, *Legendre* 838 (P); Tachien-lu, *Wilson* 1240a (A, E, GH, K, W); Tung valley, *Wilson* 3920 (A, K); O-pien Hsien, *Yü* 746 (A); Juei-she Hsien, *Yü* 973 (A); Huei-li Hsien, *Yü* 1463 (A); Ping-shan Hsien, *Yü* 5458 (E). YUNNAN: Yunnan-sen distr., Pin-fa, *Cavalerie* 3887 (E, K); Likiang, Tze-li on Yangtze, *Ching* 20261 (A); Chao-tung, *Ducloux* 4942 (P); S. Chung-tien, Wu-tso on Yangtze bank, *Feng* 3266 (A); Si-chour Hsien, Ting-mann, *Feng* 12314 (A); Mar-li-po, Sze-tai-po, *Feng* 13791 (A); W. of Yunnan-fu, 25°5'N., *Forrest* 436 (E); flank of Gali Range, 25°40'N., *Forrest* 4181 (E, K); near Teng-yueh, 25°N., *Forrest* 7503 (A, E, K); Ghi-Shan, E. of Tali lake, 25°48'N., *Forrest* 13472 (E, K); Shweli-Salwan divide, 25°6'N., 98°30'E., *Forrest* 29566 (E); Dsolin-ho, *Handel-Mazzetti* 6106 (M, W); Mengtsz, *Henry* 9623A (A, E); Feng Chen Lin, S. of Red R., *Henry* 10510B (E); near Yunnan-sen, *Maire* 816/1914 (E); Tsu-yung, *McLaren's Collectors* AA-130

(E); Pa-pien Ho, between Mohei and Maokai, *Rock* 2991 (A, UC, US); high plateau between Likiang and Tali-fu to foot of Likiang Snow Range, *Rock* 3210 (A, US); Lotueshan, W. of Yangtze bend at Shiku, *Rock* 8475 (A, UC, US); N. of Yunnan-fu, between Schi-lung-pa and Ta-sung-tchu, *Schneider* 352 (A); between Poloti and Yungpeh, *Schneider* 1690 (A, E, K); Yi-liang Hsien, *Tsai* 52136 (A, E); Yung-jen Hsien, *Tsai* 52794 (A); Kienshuei Hsien, *Tsai* 53049 (A); Shih-ping Hsien, *Tsai* 53352 (A, E in part); Ta-li Hsien, *Tsai* 53876 (A, E in part); Shang-pa Hsien, *Tsai* 54393 (A); Ping-pien Hsien, *Tsai* 55075 (A, E); Lung-ling Hsien, *Tsai* 55672 (A, E); Lan-ping Hsien, *Tsai* 56216 (A); Tung-lung-tang, Cheng-kiang, *Tsaing & Wang* 16312 (A); Wei-si Hsien, *Wang* 64330 (A, TAI); Chen-kang Hsien, *Wang* 72332 (A); Tsang-yuan, *Wang* 73202 (A); Fo Hai, *Wang* 73716 (A); Shunning, *Yü* 16611 (A, E); Mienning, Poshang, *Yü* 17896 (A, E); Mekong-Salwin divide, Alulaka, *Yü* 19099 (A, E). **Burma:** Hpiman Hill, *R. F. & Cox* 896 (E); Black Rock-Tang-tung rd., *Kermode* 17246 (K); Htawgaw, Naung-chaung Valley, Lashi country, *Ward* 1546 (E); Naung-chaung Valley, *Ward* 1701 (E). **India.** MEGHALAYA: Khasia Hills, Shillong, *Burkill & Banerjee* 50 (E); Khasia, *Herb. Griffith* 3484/2 (GH, GOET, K, M, S, W), *J. D. Hooker & Thompson s.n.*, 2 Oct. 1850 (K); Khasya and Jaintia Hills, Nongstoin, *Panigrahi* 16505 (L).

3f. *Lyonia ovalifolia* (Wallich) Drude var. *foliosa* (Fletcher) Judd, comb. et stat. nov.

Xolisma foliosa Fletcher, *Kew Bull.* 1936: 40. 1936. *Lyonia foliosa* (Fletcher) Sleumer, *Dansk Bot. Ark.* 25: 80. 1963. TYPE: Thailand, Loi, Kao Krading, ca. 1200 m. alt., 12 March 1924, *Kerr* 8673 (holotype, E!; isotype, E!).

Deciduous to semi-evergreen shrub to 1–2(–4) meters tall. Buds 1–6 by 1–4 mm. Leaf blades elliptic to slightly ovate or obovate, 2.5–6(–7) by 1.4–3.3 cm.; mesophyll with 1 or 2 layers of lignified cells near abaxial epidermis; apex abruptly short-acuminate, to acute or rounded with small mucro; base narrowly cuneate to rounded or rarely cordate; venation eucamptodromous, 2° veins smoothly arching toward margin; abaxial surface neither papillose nor glaucous, light- or yellowish-green, glabrous; petiole 2–8 mm. Inflorescences (2–)3–7.5(–11) cm. long, usually with 3 to 9 rather large, leaflike bracts 0.8–4 cm. long near lower portion or scattered throughout. Calyx lobes 2.5–5(–6) by 0.8–1.5 mm.; corolla cylindrical, (6–)7–10(–11) by 3–5.5 mm.; filaments 5–6 mm. long, with 2 spurs to ca. 0.5 mm. long. Capsule short-ovoid or ovoid, 2.5–4 by 3–4.5 mm., with 5 pale, quite thickened sutures that in dehiscence remain attached to an adjacent valve. (FIGURE 24; see also Stevens, 1970, 1971.)

DISTRIBUTION AND ECOLOGY. Limited to sandstone plateau atop Poo Krading and near Wang-sa-phung in northern Thailand (MAP 7). Common in open savannas of *Pinus merkusii* and *P. insularis*, along with *Quercus*, many grasses, and sedges; ca. 1045–1300 m. alt. Flowering November through May.

REPRESENTATIVE SPECIMENS. **Thailand:** Prov. Loey, Phu Krading, *Abbe et al.* 9400 (A, L), *Smitinand* 309 (A), 16°52'N., 101°52'E., *van Beusekom et al.* 4500 (K, L); Loei, Wang-sa-phung, *Dee* 305 (L).

3g. *Lyonia ovalifolia* (Wallich) Drude var. *rubrovenia* (Merr.) Judd, Jour. Arnold Arb. **60**: 491. 1979.

Pieris rubrovenia Merr. Philip. Jour. Sci. **23**: 256. 1923. *Lyonia rubrovenia* (Merr.) Chun, Sunyatsenia **4**: 254. 1940. TYPE: China, summit of Five Finger Mt., ca. 1900 m. alt., 1 May 1922, *McClure*, C.C.C. 9380 (holotype, PNH, not seen, photos at A, GH; isotypes, A (2 sheets)!, E!, NY (2 sheets)!, UC!, US!).

Pieris annamensis Dop in Lecomte, Fl. Gén. Indo-chine **3**: 726. 1930. *Lyonia annamensis* (Dop) Merr. Jour. Arnold Arb. **23**: 188. 1942. TYPE: Annam [Vietnam], Nha-trang, 1900 m. alt., 21 May 1922, *Poilane* 3580 (holotype, P!; fragment of holotype, L!).

Pieris obliquinervis Merr. & Chun, Sunyatsenia **5**: 157. 1940. TYPE: China, [prov. Kwangtung], Hainan Is., Ting-On distr., Mo-Cheung, 30 Dec. 1933, *C. Wang* 35986 (holotype, A!; isotypes, NY!, IBSC?, not seen).

Semi-evergreen shrub to ca. 5 meters tall. Buds 1–6 by 1–4.5 mm. Leaf blades obovate, ovate, elliptic, or narrowly elliptic (3–)4–9(–10) by 0.8–2.6(–3) cm.; mesophyll with 1 or 2 layers of lignified cells near abaxial epidermis; apex acuminate to acute (or obtuse); base narrowly cuneate to rounded; venation eucamptodromous to slightly brochidodromous toward apex, 2° veins smoothly arching toward margin; abaxial surface neither papillose nor glaucous, usually shiny yellowish to golden-green (occasionally reddish due to long-headed hairs), glabrous; petiole 6–11 mm. long. Inflorescences 2.5–7(–11) cm. long., with small bracts 2.5–7 mm. long throughout. Calyx lobes (2–)2.5–4 by 0.8–1.9 mm.; corolla cylindrical to elongate-urceolate, 5–7 by 3–3.5 mm.; filaments 3–4 mm. long, with 2 spurs to 0.2 or 0.3 mm. long. Capsule subglobose to globose, 2.5–4 by 3–4.5 mm., with 5 pale, slightly thickened sutures that in dehiscence remain attached to an adjacent valve or split irregularly. (FIGURE 25; see also Lecomte (1930), Anonymous (1974b).)

DISTRIBUTION AND ECOLOGY. Hainan and Vietnam (MAP 7). Woods, moist, dense forests, thickets, mountain ridges, often with pines; ca. 900–1900 m. alt. Flowering December and May.

REPRESENTATIVE SPECIMENS. **China.** KWANGTUNG. Hainan Is.: Fan Yah, Five Finger Mt., *Chun & Tso* 44099 (A, B, PE, US); Bi-sha, *Hainan Expedition Team* 759 (PE); Loktung, *Lau* 27266 (A); without definite locality, *Wang* 35569 (US). **Vietnam.** Nha-trang, *Poilane* 3574 (A, B, P).

Lyonia ovalifolia is most closely related to *L. villosa*, which occurs chiefly at higher elevations (FIGURE 7). It differs from *L. villosa* in its larger and more commonly acuminate-tipped leaves, usually longer racemes, cylindrical flowers, and filaments with two spurs below the anther-filament junction.

Variation within Lyonia ovalifolia. Populations of *Lyonia ovalifolia* are separable into several morphologically distinct and geographically and/or ecologically isolated varieties. These varieties can be arranged into two groups based upon morphological and anatomical characters. *Lyonia ovalifolia* vars. *elliptica*, *hebecarpa*, and *doyonensis* are very similar and tend to have deciduous leaves with the secondary veins \pm brochidodromous, sinuous or \pm irregular,

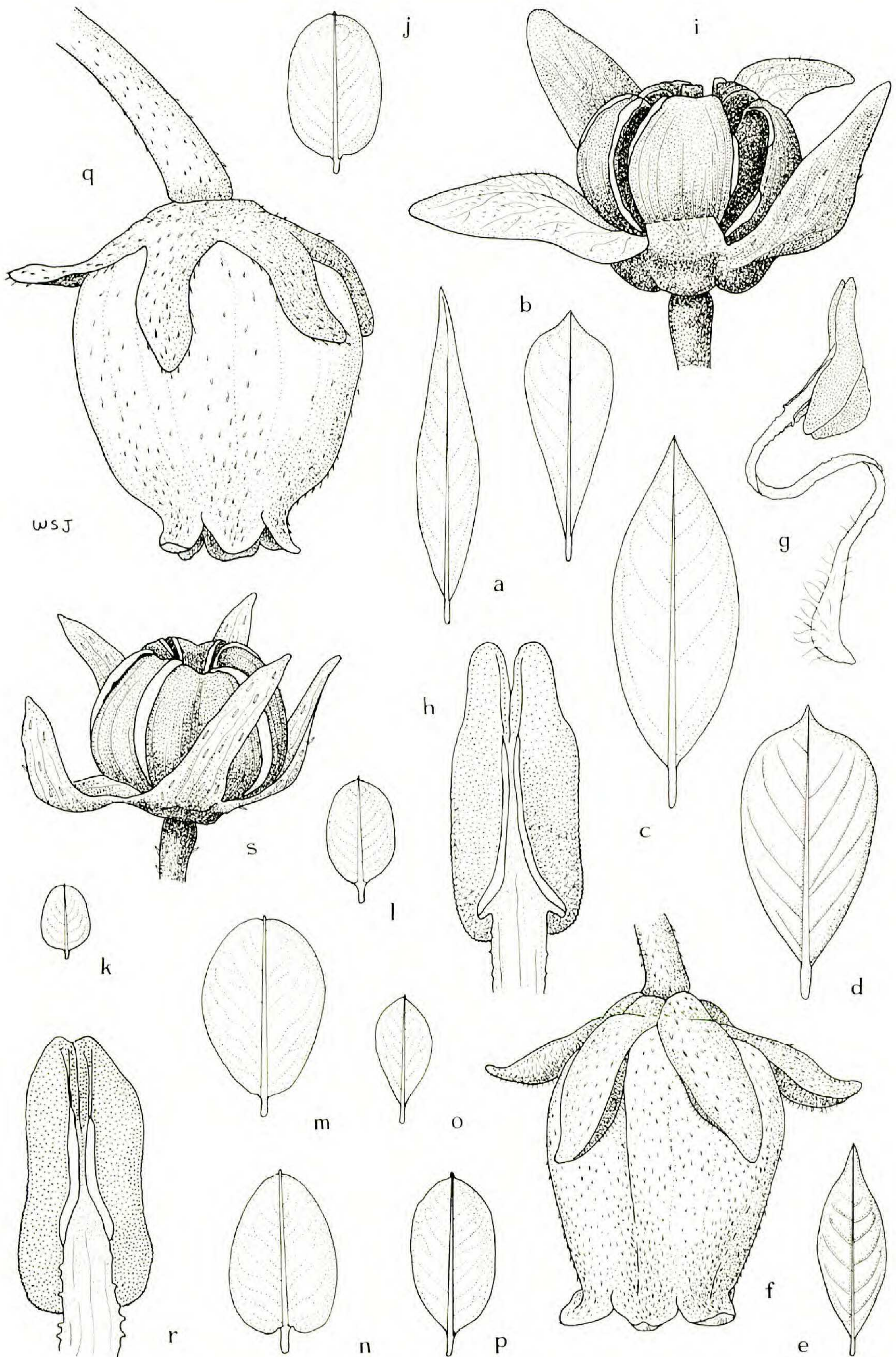


FIGURE 25. a-i, *Lyonia ovalifolia* var. *rubrovenia*: a-e, leaves, $\times .5$; f, flower, $\times 6$; g, stamen, $\times 12.5$; h, anther, $\times 25$; i, capsule, $\times 6$. j-s, *L. villosa* var. *sphaerantha*: j-p, leaves, $\times .5$; q, flower, $\times 6$; r, anther, $\times 25$; s, capsule, $\times 6$.

and of varied strengths (i.e., intersecondary veins common) and angles of divergence from the midvein. The cells of the spongy mesophyll of the lamina are never lignified, and the calyx lobes tend to be very short. The capsules are globose to subglobose. In contrast, *L. ovalifolia* vars. *lanceolata*, *foliosa*, and *rubrovenia* have more coriaceous, deciduous to semi-evergreen leaves with the secondary veins \pm eucamptodromous, \pm uniform, and smoothly arching toward the margin. One or two layers of cells of the spongy mesophyll just above the abaxial epidermis are usually lignified, and the calyx lobes are usually elongated. The capsules are subglobose or globose to conspicuously and quite narrowly ovoid or short-ovoid. The abaxial leaf epidermis is usually a characteristic yellowish gold or yellowish green color upon drying. *Lyonia ovalifolia* var. *ovalifolia* fills the morphological gap between the two groups. It has deciduous to semi-evergreen leaves with the secondary veins usually smoothly arching toward the margin but with the mesophyll cells never lignified. Its calyx lobes are very small, except in populations from the western Himalayas, and its capsules are subglobose to globose.

There has been much confusion concerning the geographic range of *Lyonia ovalifolia* var. *elliptica*, from Japan and Taiwan, and the identity of plants referred to here as var. *hebecarpa*, which occurs in eastern China (see MAP 6). Nakai (1919) and Hara (1966) considered var. *elliptica* to be endemic to Japan, while Sargent (1913), Rehder (1924), Handel-Mazzetti (1936), and Ohwi (1965) thought that it also occurred in Taiwan and/or eastern China. Sargent (1913), Rehder (1924), and especially Hara (1966) very properly pointed out that var. *elliptica* (= subsp. *neziki*) differs from the related Himalayan and western Chinese plants (i.e., var. *ovalifolia*, as considered here) in its much thinner and smaller leaves with different secondary veins, its slightly smaller capsules and corollas, and its shorter racemes. But the situation was confused by these widely varying treatments of the plants of eastern China and Taiwan, and even Hara, who treated all related plants of the Himalayas, China, and Taiwan as *L. ovalifolia* subsp. *ovalifolia*, stated (1966, p. 648) that "some intermediate forms [i.e., between var. *elliptica* and var. *ovalifolia*] occur in China and Formosa." Although when compared to the Japanese plants, those of Taiwan tend to have slightly larger, less pubescent leaves, longer inflorescences and calyx lobes, and more often glabrous bud scales, the range of overlap in these characters is great, and the plants of the two islands cannot be consistently separated using these or any other morphological characters. Both also have the very characteristic \pm dense tuft of long-unicellular hairs near the leaf base, which is not found in any other variety of *L. ovalifolia*. In contrast, the Taiwanese and Japanese populations are clearly distinguishable from those of such provinces as Chekiang, Fukien, and Kiangsi by the above-mentioned leaf pubescence pattern. In addition, they often have slightly smaller leaves, shorter racemes, and smaller flowers. The eastern Chinese plants are not only clearly different from the populations of Japan and Taiwan, but they are also distinguishable from the Himalayan plants, as previously mentioned. In fact, these differences were used by Sargent and Rehder in separating var. *ovalifolia* from their more inclusive var. *elliptica*. Thus, I consider *L. ovalifolia* var. *elliptica* to be endemic to Japan and Taiwan and refer the eastern China "intermediate

forms" of Hara (1966) or the eastern China "var. *elliptica*" of Sargent (1913) or Rehder (1924) to the closely related var. *hebecarpa*.

Lyonia ovalifolia var. *hebecarpa* is essentially geographically isolated from both vars. *doyonensis* and *ovalifolia*, although the ranges of *hebecarpa* and *doyonensis* overlap slightly in northwestern Yunnan (compare MAPS 5 and 6), and *hebecarpa* and *ovalifolia* occur sympatrically in parts of Yunnan and western Kwangsi. In Yunnan altitudinal and ecological differences may also play a part in isolating these taxa: here var. *hebecarpa* occurs chiefly between ca. 2300 and 3300 meters, with var. *ovalifolia* from ca. 1100 to 3050 meters.

In northwestern Yunnan, where all three taxa occur together, specimens are often difficult to determine to variety, and hybridization probably takes place. Occasional puzzling and completely intermediate plants have been collected; for example, *Wang 64013* (Weisi Hsien, 3500 m.; A, TAI), *Henry 9091, 9091D* (Mengtze [Mengtzu]; A, E), and *Forrest 24356* (Shweli-Salwin divide, 8000–9000 ft.; E, K), all from Yunnan, are clearly intermediate between *Lyonia ovalifolia* vars. *hebecarpa*, *ovalifolia*, and/or *doyonensis*. In addition, there is a specimen (*R. A. 1658* (E!)), probably from northern Burma) that is intermediate between vars. *ovalifolia* and *doyonensis* in leaf shape and venation characters. It is likely that all three taxa interbreed freely where they come into contact, and intermediate specimens seem to be completely fertile. It is often very difficult even to infer the exact parentage of these intermediate plants from herbarium specimens alone, and the situation needs to be thoroughly investigated in the field. A few specimens (placed here in var. *ovalifolia*) collected from high elevations in Sikkim and Nepal (e.g., *Smith & Cave 2718* (B, UC), and *Stainton, Sykes, & Williams 2870* (A, E)) also approach var. *doyonensis* in leaf shape and in prominence of secondary and tertiary veins.

Lyonia ovalifolia var. *hebecarpa* is quite variable in the shape and size of its leaves (see FIGURE 21); the amount and distribution of unicellular hairs on its leaves, capsules, and bud scales; the amount of glaucousness on the abaxial leaf surface; and the size of its flowers and fruits. The variability is greatest in Yunnan. As in var. *elliptica*, the leaves produced early in the growing season are frequently more strongly cordate than later-formed ones. In the fall the leaves often become reddish on the adaxial surface before dropping.

Lyonia ovalifolia var. *doyonensis* (a rare and local taxon) is in general aspect intermediate between vars. *hebecarpa* and *ovalifolia*; it is, however, immediately recognizable and differs from both in its large leaves with truncately short-acuminate apices, prominently abaxially raised secondary and tertiary veins, and length/width ratios of ca. 0.9–1.3(–1.5). In addition to the above characters, var. *doyonensis* differs from var. *hebecarpa* in its obscurely to clearly papillose abaxial leaf surfaces, and from var. *ovalifolia* in the often more irregular secondary veins.

Field work is necessary to determine the factors isolating *Lyonia ovalifolia* var. *doyonensis* from var. *ovalifolia*. Since in Yunnan var. *doyonensis* tends to occur above ca. 2500 meters and var. *ovalifolia* commonly grows down

to ca. 1200 meters, the two may be at least partially ecologically isolated.

As mentioned above, *Lyonia ovalifolia* var. *ovalifolia* is closely related to vars. *doyonensis* and *hebecarpa*; importantly, it also forms the connecting link between these varieties and var. *lanceolata*.

In Yunnan and adjacent areas *Lyonia ovalifolia* var. *ovalifolia* can be distinguished from var. *hebecarpa* by its differently shaped, more coriaceous, and often abaxially papillose leaves with more smoothly arching secondary veins, and from var. *doyonensis* by the length/width ratio of its leaves, by its more elongate and gradually acuminate leaf apices, and by its less prominently abaxially raised secondary and tertiary leaf veins.

This taxon is more variable than any other variety of *L. ovalifolia*, possibly because of the diversity of habitats in which it occurs and its very broad geographic range. Part of this variation is probably due to environmental or developmental factors; thus, plants in exposed and/or dry areas tend to have smaller leaves, and leaves produced early in the season tend to have more strongly cordate bases than those produced later. However, much is probably genetic (for example, variation in length of calyx lobes, appearance of the abaxial leaf epidermis, presence of papillae, and—to some extent—leaf shape) and correlates well with geography.

Lyonia ovalifolia var. *ovalifolia* is easily distinguished from var. *lanceolata* in Yunnan and adjacent regions, where the two occur sympatrically, by its often longer inflorescences, shorter calyx lobes, usually more globose or subglobose capsules, and more ovate and/or cordate leaves lacking a lignified layer of mesophyll cells just beneath the often glaucous and/or papillose abaxial epidermis. Plants of *L. ovalifolia* var. *ovalifolia* collected from northwestern India and some areas of Nepal, Bhutan, and Assam (especially at lower elevations) are much more similar to var. *lanceolata*, but even these plants can be distinguished (although sometimes only with difficulty) by their usually more globose or subglobose capsules, often slightly shorter calyx lobes, and more frequently cordate-based leaves that are slightly wider in relation to their width and that lack lignified mesophyll cells.

In northwestern India, Pakistan, Nepal, Bhutan, and Assam, there are plants that produce flowers with characteristically elongated calyx lobes ((1.5–)2–3(–4) mm.) and subglobose to globose capsules; the leaves are ovate to slightly cordate (less commonly, more or less elliptic), often dry a shiny bluish green color, and usually lack both papillae and a glaucous layer on the abaxial surface. These forms grade imperceptibly into plants with often larger, more consistently cordate to ovate, often abaxially glaucous and/or papillose leaves and slightly longer inflorescences as one moves to populations at increasingly higher elevations in the Himalayas. Papillose and/or glaucous specimens become common above ca. 2100 meters. As one travels eastward from Pakistan and northwestern India through Nepal, Bhutan, and Assam, into Burma, Thailand, Indochina, and Yunnan, the average length of the calyx lobes decreases from (1.5–)2–3(–4) mm. in northwestern India to only (1–)1.5–2(–2.5) mm. in Yunnan. In addition, the leaves become more frequently papillose and/or glaucous and more consistently cordate-ovate, and the inflorescences more elongated. Extreme forms characterized by very small

calyx lobes, long racemes, and often papillose and glaucous leaves occur in Yunnan and western Kwangsi, while plants from Thailand and Indochina sometimes have slightly irregular secondary veins toward the leaf apices. Thus, plants from the eastern portions of the range of var. *ovalifolia* (Yunnan, Kwangsi, Indochina, and Thailand) tend to resemble plants from the higher elevations in the Himalayas further west. It is thus much easier to differentiate vars. *ovalifolia* and *lanceolata* in Yunnan, where they come into contact, than it is to separate a specimen of var. *ovalifolia* collected in northwestern India from a specimen of var. *lanceolata* from Yunnan or Szechwan. *Lyonia ovalifolia* var. *ovalifolia* is probably chiefly geographically isolated from var. *lanceolata* although the factors isolating this taxon are in need of further investigation, especially since the varieties are more different morphologically when they occur sympatrically (in Yunnan) than they are when they occur separately!

The situation is complicated by the existence of a disjunct population of *Lyonia ovalifolia* var. *lanceolata* in the Khasia Hills of Assam (India). Many plants from this locality are indistinguishable from individuals of var. *lanceolata* collected from Yunnan, Szechwan, or Kweichow, yet they seem to intergrade completely with individuals of var. *ovalifolia*, which is the more characteristic variety of *L. ovalifolia* west of the Yunnan-Burma border (see Griffiths 314 (GH, K, W); *Bot. Gard. Calcutta s.n.* (E, L); *Hooker & Thomson s.n.*, Nov. 1850 (E, K)). The explanation of this situation awaits further field studies.

In conclusion, it seems best (and most useful) to recognize *Lyonia ovalifolia* vars. *ovalifolia* and *lanceolata* as distinct taxa, in spite of their intergradation in the Khasia Hills, because 1) where they occur sympatrically in Yunnan, they are very different and do not seem to hybridize extensively; and 2) they have well-defined geographic ranges that overlap only slightly in Yunnan and Kwangsi, and within which they can usually be easily distinguished. In contrast, the high-elevation Himalayan and Yunnanese forms of *L. ovalifolia* var. *ovalifolia* have not been given formal taxonomic recognition as distinct from the low-elevation western Himalayan forms because these intergrade so completely across such an extensive geographic area that separating them would be completely arbitrary. They are thus maintained within a single variety, although it is recognized that the amount of morphological variation within this taxon is greater than that separating some other varieties of *L. ovalifolia*, such as vars. *lanceolata* and *foliosa*, or *hebecarpa* and *elliptica*. However, these varieties can be recognized since they are separated by a consistent and geographically correlated morphological gap.

Lyonia ovalifolia var. *lanceolata* is most closely related to vars. *rubrovenia*, *foliosa*, and *ovalifolia*. It can be differentiated from var. *rubrovenia* by its larger flowers; inflorescences usually with well-developed, leafy bracts; and capsules with more strongly thickened sutures. In addition, it tends to have less strongly lignified mesophyll cells. It can be distinguished from var. *foliosa* by its larger leaves with acuminate apices, inflorescences with leafy bracts usually limited to the base, and slightly larger capsules. Both of these varieties are geographically isolated from var. *lanceolata* (see MAP 7). *Lyonia ovalifolia* var. *lanceolata* is usually easily distinguished from var. *ovalifolia* by its

narrower leaves with cuneate to rounded bases and yellowish green abaxial surfaces, its often differently shaped capsules, its longer calyx lobes, and its shorter racemes.

Lyonia ovalifolia var. *lanceolata* is most variable in Yunnan, where forms with very large, very small, densely pubescent, or shortly and bluntly acuminate leaves occur. Some of this variation may be the result of crossing with other varieties of *L. ovalifolia*. A few specimens of var. *lanceolata* from Yunnan show some characteristics of var. *hebecarpa*, a taxon occurring at slightly higher elevations (ca. 2300–3300 vs. 1200–2800 m.) in this province, and *Maire 1068* (vicinity of Yun-nan-sen, Yunnan (E)), *Wang 65054* (Li-kiang Hsien, 2500 m., (A)), and *Tsai 57093* (NW. Yunnan (A, E)), probably represent hybrid individuals.

In *Lyonia ovalifolia* var. *lanceolata* there are sometimes branches with quite leafy-bracted racemes at nearly every node; herbarium material of such branches often lacks true leaves, although they appear leafy (see Wallich, 1820), since the plants are deciduous and flowering occurs on branches of the previous year. The bracts are usually narrower in relation to their length than are leaves from the same plant.

Lyonia ovalifolia vars. *foliosa* and *rubrovenia* are very closely related to var. *lanceolata*. Variety *foliosa* is distinctive due to its small leaves that have short petioles and abruptly short-acuminate to acute or rounded apices with a small mucro, and its inflorescences that often have conspicuous leaf-like bracts throughout. Variety *rubrovenia* is easily distinguished by its more consistently globose or subglobose capsules with the sutures less strongly thickened; its smaller corollas, filaments, and spurs; and its racemes that lack large, leaflike bracts.

Lyonia ovalifolia var. *rubrovenia* is quite variable in the size and the length/width ratio of its leaves. Forms that have larger and narrower leaves with more numerous veins have been described as *Pieris obliquinervis*, but there is complete intergradation between these plants and those with shorter and more abruptly acuminate leaves.

Nomenclature. The specimen at Leiden (Herb. no. 167) that Sleumer labeled as the type (i. e., lectotype) of *Andromeda elliptica* cannot have been a specimen on which the original description was based because it consists of two twigs in fruit and one with very young inflorescences—Siebold and Zuccarini (1846) described the twigs, leaves, inflorescences, and flowers, but not the fruits. Neither are two possible duplicates (also at L) likely to be type material: one (Herb. no. 168) is composed of one sterile twig, two twigs with mature capsules, and one small flowering scrap of a *Vaccinium*; the second (Herb. no. 169) includes one branch with mature capsules, and another with floral buds and newly opened flowers (nearly all with corollas smaller than the measurements given in the description). On all three sheets the most obvious feature of the plant is the presence of these characteristic subglobose capsules with pale, very thick sutures, and it is unlikely that Siebold and Zuccarini would have overlooked such a prominent part of the plant while describing the flowers in minute detail. The lectotype should probably be selected from

material sent to Siebold by H. Burger in 1842 (see earlier).

Pieris henryi Lévl. is probably best placed in synonymy under *Lyonia ovalifolia* var. *hebecarpa*, instead of under *Lyonia villosa* var. *pubescens* as was done by Rehder (1934). Its filaments have two spurs just below the junction with the anther, a condition not found in *L. villosa* but characteristic of *L. ovalifolia*. Also, its 2–2.5 mm. long calyx lobes would be anomalous in *L. villosa* var. *pubescens* (in which they are 2.5–5.5 mm. long), although they are within the normal range of variation of *L. ovalifolia*. Within *Lyonia ovalifolia*, its chartaceous, deciduous leaves, with their secondary veins \pm irregular to sinuous and with a sparse covering of short, unicellular hairs abaxially along the midvein and many secondary veins, indicate an affinity with var. *hebecarpa*. According to a note on the type sheet (*A. Henry 9681*), J. Hutchinson also referred *Pieris henryi* to *L. ovalifolia*. This specimen is unusual because its mucronate-tipped leaves are only ca. 4 cm. long. Such small-leaved individuals (or populations?) also occur in several other varieties of *L. ovalifolia* in Yunnan.

Pieris ovalifolia var. *tomentosa* was described by Fang (1938) from a specimen on which nearly every part of the plant is more or less densely covered with unicellular hairs. The leaves have abruptly acuminate apices and smoothly arching secondary veins, the racemes are rather short (3–6.5 cm.), and the calyx lobes are only 2–2.5 mm. long. In Yunnan occasional specimens of *Lyonia ovalifolia* var. *lanceolata* (e.g., *Maire 1064*) have been collected that are nearly as pubescent, and the plant described by Fang is likely only an extremely pubescent form of this taxon.

Possible hybridization with other species. *Lyonia villosa* probably occasionally hybridizes with *L. ovalifolia* where they come into contact, and a specimen (*Rock 24400* (A, E, K, UC, US)) collected at 3800 meters in southwestern Szechwan (on Siga-shan) is morphologically intermediate. *Rock 24400* is probably a hybrid between *L. villosa* var. *pubescens* and *L. ovalifolia* var. *hebecarpa*. The differences between these two taxa and the characters of their putative hybrid are listed in TABLE 9. As can be seen, the specimen has the long calyx lobes and slightly smaller leaves of *L. villosa* and the spurs and long inflorescences of *L. ovalifolia*. Field studies are necessary to verify the identity of *Rock 24400* and to determine the causes and frequency of hybridization, as well as the isolating mechanism (probably ecological) operating.

Several collections of what may be hybrids between *Lyonia ovalifolia* (probably var. *ovalifolia*) and *L. villosa* (possibly var. *sphaerantha*) have been collected from rather high elevations in northern Burma and Yunnan (i.e., Burma, N. Triangle (Tama Bum), Kachin state, 9000–10,000 ft., *Ward 21101* (A, E); China, Yunnan, Salween-Kiukiang Divide, Wangtzang, 2600 m., *Yü 20214* (A, E); [Burma?], Chou-chi woods, 10,000 ft., *R. A. 1742* (E); [Burma?], Meku-ji Pass, 10,000 ft., *R. F. 1819* (E)). These plants are characterized by leaves that are strongly to only slightly cordate, 5–9.5 by 3–5.8 cm., with abruptly long-acuminate apices (the acumen often curved and/or folded over in pressing), and more or less brochidodromous and slightly irregular secondary veins. The abaxial surface is not papillose and

TABLE 9. A comparison of *Lyonia villosa* var. *pubescens*, *L. ovalifolia* var. *hebecarpa*, and their probable hybrid.

CHARACTER	<i>L. ovalifolia</i> var. <i>hebecarpa</i>	<i>Rock 24400</i> (probable hybrid)	<i>L. villosa</i> var. <i>pubescens</i>
LEAF LENGTH	5-12.5(-15) cm.	4.5-8 cm.	(2.5-)3-7(-8.5) cm.
LEAF APEX	Acuminate to long-acumi- nate	Slightly acuminate	Acute to rounded with mucro, or short-acuminate
ABAXIAL LEAF EPIDERMIS	Glaucous or not	Glaucous	Usually glaucous
2 SPURS NEAR APEX OF FILAMENT	Present	Present	Lacking
RACEME LENGTH	(2.5-)3.5-12(-16) cm.	4.5-11 cm.	1-4(-6) cm.
CALYX LOBE LENGTH	1-2.5(-3) mm.	2.5-3.5 mm.	(2-)3-5(-6.5) mm.
ELEVATION	Ca. 900-3300 (-3800) m.	Ca. 3800 m.	Ca. (1800-)2300- 3800(-4100) m.

usually has rust-colored veins due to a dense covering of ferruginous, multicellular, long-headed hairs. The racemes are usually 4-9.5 cm. long and have several large, leaflike bracts near the base. The corollas are 5-7.5 mm. long, the calyx lobes are 1.5-2.5 mm. long, and the filaments are without spurs. The capsules are subglobose to globose, to ca. 3 by 4 mm., with only slightly thickened sutures. Although it is difficult to determine the origin of these plants without field and crossing studies, they are probably hybrids between *L. ovalifolia* and *L. villosa* since they have the unappendaged filaments and more or less irregular secondary veins of *L. villosa*, along with the large, acuminate-tipped leaves and elongated, leafy inflorescences of *L. ovalifolia*. In addition, they have only been collected in regions (and at elevations) where both taxa can be expected to occur.

4. *Lyonia villosa* (Wallich ex Clark) Hand.-Mazz. Symb. Sin. 7: 789. 1936.

Deciduous low shrub to small tree to 3.5(-9) meters tall with brownish to gray, longitudinally furrowed bark, sometimes spreading vegetatively by horizontal underground rhizomes. Twigs terete to slightly ridged, slender to less commonly stout, sometimes with few long-headed hairs, otherwise glabrous to densely pubescent. Buds elongate-ovoid, 1-13 by 1-4 mm., often reddish. Leaf blades elliptic to slightly ovate, obovate, or nearly orbicular, (1.8-)2.5-8.5(-10) by (1-)1.5-5(-5.5) cm., ± flat, ± chartaceous to slightly coriaceous, ca. 0.1-0.3 mm. thick, often turning reddish in autumn; apex acute, obtuse to rounded with short to elongated (to ca. 4 mm.) mucro, or short-acuminate; base usually broadly cuneate to slightly cordate; margin

entire, plane to slightly revolute; venation brochidodromous (to slightly eucamptodromous near base), with 3° veins percurrent to reticulate; adaxial surface with sparse long-headed hairs, otherwise often glabrescent, sparsely to densely pubescent on midvein, sometimes extending to 2° veins, the 3° and higher order veins obscure to slightly visible, the 2° veins sometimes slightly depressed; abaxial surface strongly to obscurely papillose or ± smooth, usually glaucous, with sparse long-headed hairs, otherwise glabrous to densely pubescent along midvein, sometimes extending to many 2° (and occasionally even 3°) veins, the 3° and higher order veins obscure to slightly visible, the 2° veins slightly raised and visible, ± sinuous or irregular; petiole 2–13 mm. long, with long-headed hairs, otherwise pubescent adaxially or all around. Flower buds usually below vegetative buds; inflorescences racemose, to 6- to 12- (to 18-)flowered, (0.5–)1–4(–7) cm. long, horizontal to slightly ascending; flowers pendulous and secund. Pedicels usually slender, 2.5–8.5(–10) mm. long, with long-headed hairs, otherwise glabrous to densely pubescent; bracteoles opposite, basal, narrowly triangular to linear, 1–5 mm. long; bracts extremely variable, usually 1 to 4 large and leaflike near base of raceme or scattered throughout (but inflorescence often appearing leafy throughout due to its shortness), the others small, similar to bracteoles in shape, usually caducous. Flowers 5-merous; calyx lobes narrowly triangular to linear, with slightly acuminate, acute to rounded apices, (2–)3–5(–6.5) by 0.5–1.8(–2) mm., the adaxial side often with few long-headed hairs, otherwise glabrous to densely pubescent, the abaxial side with scattered long-headed hairs, otherwise glabrous to densely pubescent; corolla cylindrical to urceolate, 4.5–9(–11) by 3–7.5(–8) mm., white and sometimes slightly pink tinged, abaxially with sparse to moderate long-headed hairs; filaments with long-unicellular hairs, especially near base, 3.5–6 mm. long, unappendaged, anthers 1.1–1.6 mm. long; ovary glabrous to sparsely or less commonly moderately pubescent, placentae subapical to central. Capsule ovoid to short-ovoid to globose or subglobose, sometimes with apex slightly constricted, 2.5–4(–4.5) by 3–4.7(–6) mm., usually lacking long-headed hairs, otherwise glabrous to sparsely pubescent, with pale, thickened sutures that in dehiscence usually remain attached to an adjacent valve; seeds 0.7–1.1 mm. long.

DISTRIBUTION. In an arc from southwestern Szechwan and northern Yunnan (China), westward to Nepal and northwestern India; various habitats, ca. (1800–)2300–3800(–4100) m. alt.

Key to the Varieties of *Lyonia villosa*

1. Pedicels usually glabrous or with few short, curled hairs toward base; corollas urceolate, 4.5–6.5(–7) mm. long; leaves usually 2–4.5 cm. long, abaxial surface strikingly papillose, with midvein and secondary veins glabrous; [chiefly Yunnan, northern Burma, and southeastern Tibet]. 4b. var. *sphaerantha*.
1. Pedicels very slightly to densely pubescent; corollas urceolate to cylindrical, 4.5–9(–11) mm. long; leaves (3–)3.5–8.5(–10) cm. long, abaxial surface at most slightly papillose, with veins pubescent or not.
 2. Corollas urceolate, 5.5–8 by 4.5–7.5(–8) mm.; abaxial leaf surface usually

- ± papillose, glabrous on veins; pedicels very sparsely to moderately covered with short, usually much-curved, unicellular hairs; capsules subglobose to short-ovoid, apex not constricted; [Bhutan, Sikkim, Nepal, and northern India]. 4a. var. *villosa*.
2. Corollas cylindrical to occasionally urceolate, (4.5-)6.5-9(-11) by 3-4.5(-6) mm.; abaxial leaf surface often epapillate, occasionally obscurely papillose, often pubescent on midvein or secondary veins; pedicels moderately to densely covered with long, erect to curled, unicellular hairs; capsules ovoid to subglobose, apex often slightly constricted; [southeastern Tibet, Szechwan, and northern Yunnan].
. 4c. var. *pubescens*.

4a. *Lyonia villosa* (Wallich ex Clark) Hand.-Mazz. var. *villosa*

Pieris villosa Wallich ex Clark in J. D. Hooker, Fl. Brit. India 3: 461. 1882. *Andromeda villosa* Wallich, Catal. Indian Pl. 762. 1829, *nomen nudum*. *Xolisma villosa* (Wallich ex Clark) Rehder, Jour. Arnold Arb. 5: 1924. TYPE: Nepal, *Andromeda* 762, Aug. 1821, *N. Wallich s.n.* (lectotype, K-W (IDC 7394. 90: I. 8!)).

Deciduous shrub to small tree to 3.5(-9) meters tall. Twigs glabrous to very sparsely pubescent. Buds glabrous. Leaf blades (3.5-)4-8(-10) by (2-)3-5.3 cm.; apex acute to rounded with short (to ca. 4 mm.) mucro; abaxial surface usually papillose or obscurely so (occasionally lacking papillae) and glabrous; petiole 5-13 mm. long, adaxially pubescent. Inflorescences 1.5-4(-7) cm. long. Pedicels very sparsely to moderately and usually short-crisped-pubescent. Calyx lobes (3-)3.5-5(-6) mm. long, abaxial surface usually glabrous; corolla urceolate, 5.5-8 by 4.5-7.5(-8) mm.; ovary glabrous. Capsule subglobose to short-ovoid, 3-4(-4.5) mm. long, glabrous. (FIGURE 26.)

DISTRIBUTION AND ECOLOGY. Nepal to Bhutan and adjacent areas of northern India and Tibet (MAP 8). *Rhododendron* forests and thickets, mixed temperate forests, *Betula utilis* forests, *Pinus* and/or *Quercus* forests, mixed forests in which *Pinus excelsa* is locally dominant, open woods and ridges (see Stainton, 1972); ca. (2150-)2750-3800(-3950) m. alt. Flowering chiefly May through July, probably peaking in June.

REPRESENTATIVE SPECIMENS. **China.** TIBET: Yatung, 27°51'N., 88°35'E., *Hobson s.n.*, 1897 (K). **Bhutan:** Tashing, *Cooper 1515* (E); Phajudin Thimphu, *Cooper 2543* (E); Paro, *Cooper 3568* (E); Dumthang, Ha Valley, *Ludlow & Sherriff 46* (E); Bela La near Pan, *Ludlow & Sherriff 163* (E). **Nepal:** Dor-Tinjure-Tinjure Phedi-Chauke, *Kanai et al. 726636* (TI); Suke-Kokim Pokhari-Hati Surde-Hile Chok, *Kanai et al. 726637* (TI); Khumbu, Khumzung, *Poelt s.n.*, 5 Oct. 1962 (M); Langtang Valley, *Polunin 539* (E); Khaptar forest, *Ram 511* (A); Thogundanda-Kaligad, *Shrestha 4188* (US); Lete, S. of Tukucha, Kali Gandaki, *Stainton et al. 974* (E); Sauwala Khola, *Stainton et al. 3020* (E); Bhurungdi Khola, *Stainton et al. 5808* (E); Rambrong, Lamjung Himal, *Stainton et al. 6048* (A, E); Siringdham, 22°20'N., 87°57'E., *Williams 605* (M). **India.** SIKKIM: Tonglu, *Hara et al. 69733* (TI); Lachen, *J. D. Hooker s.n.*, 29 May 1849 (K). WEST BENGAL; Darjeeling, Palmajua, *Cowan s.n.*, 4 June 1916 (E). UTTAR PRADESH: E. Almora division, Gon Valley, *Osmaston 1509* (A); Kumaon, Ruf Gap, *Strachey & Winterbottom 2* (GH).

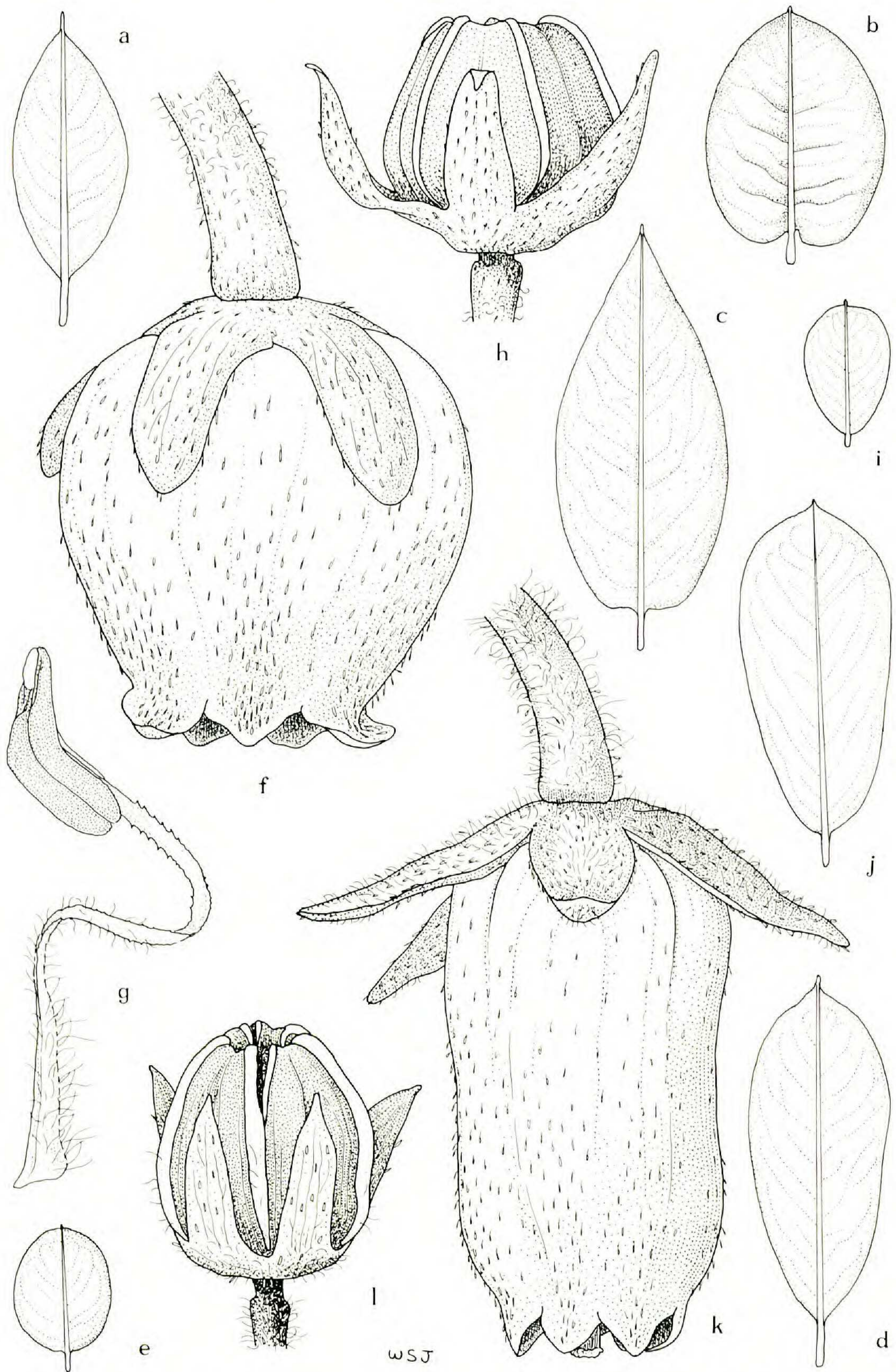
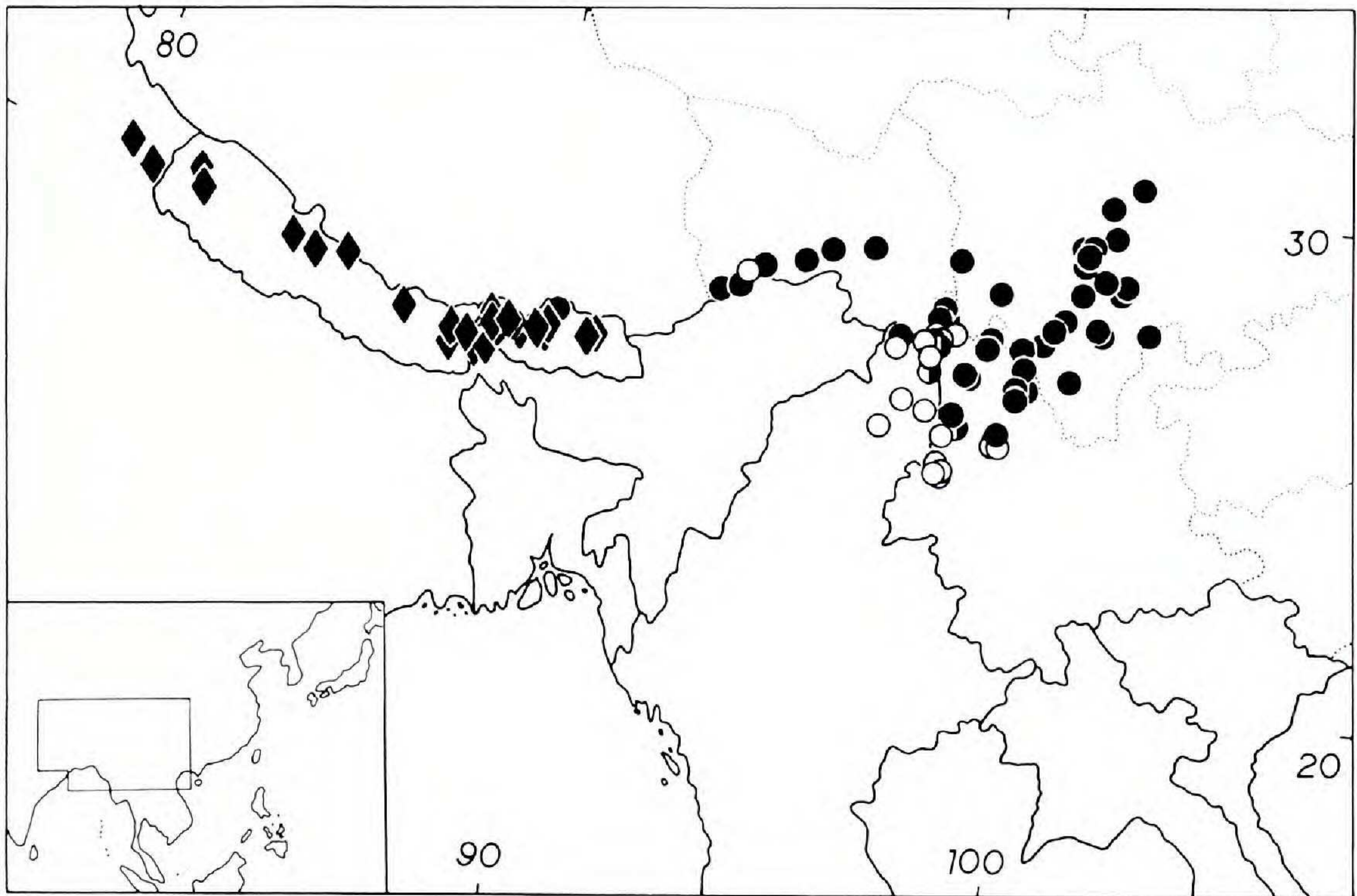


FIGURE 26. a-h, *Lyonia villosa* var. *villosa*: a-e, leaves, $\times .5$; f, flower, $\times 6$; g, stamen, $\times 12.5$; h, capsule, $\times 6$. i-l, *L. villosa* var. *pubescens* (in part): i, j, leaves, $\times .5$; k, flower, $\times 6$; l, capsule, $\times 6$.



MAP 8. Distribution of *Lyonia villosa* var. *villosa* (diamonds), *L. villosa* var. *sphaerantha* (circles), *L. villosa* var. *pubescens* (dots), and intermediates between vars. *sphaerantha* and *pubescens* (half-blackened circles).

4b. *Lyonia villosa* (Wallich ex Clark) Hand.-Mazz. var. ***sphaerantha*** (Hand.-Mazz.) Hand.-Mazz. Symb. Sin. 7: 789. 1936.

Xolisma sphaerantha Hand.-Mazz. Anzeig. Akad. Wiss. Wien Math.-Naturwiss. Kl. 62: 131. 1925. TYPE: China, prov. Yunnan, between Mekong and Salween rivers, ca. 3200–3500 m., 16 June 1916, *Handel-Mazzetti* 8918 (holotype, w!; isotypes, A!, E!).

Deciduous low to erect shrub or rarely small tree to 2.5(–4.5) meters tall. Twigs glabrous to very sparsely pubescent. Buds glabrous. Leaf blades (1.8–)2.5–4.5(–6) by (1–)1.5–3.5 cm.; apex usually obtuse to rounded with short (to ca. 2.5 mm.) mucro; abaxial surface strikingly papillose and glabrous; petiole 2–6 mm. long, adaxially pubescent. Inflorescences (0.5–)1–2.5(–3) cm. long. Pedicels glabrous or very sparsely crisped-pubescent near base. Calyx lobes (2.5–)3–4.5(–5) mm. long, abaxial surface glabrous; corolla urceolate, 4.5–6.5(–7) by 3.5–5.5(–6) mm.; ovary glabrous. Capsule subglobose to short-ovoid, 2.5–3.5(–4) mm. long, glabrous. (FIGURE 25.)

DISTRIBUTION AND ECOLOGY. Northern Burma, northwestern Yunnan, and southeastern Tibet (MAP 8). Mixed cool-temperate forests, *Pinus* or *Abies* forests, *Rhododendron* forests or thickets, rocky meadows and shrub-covered slopes and ridges; (2000–)2750–3600(–3800) m. alt. Flowering May through August, probably peaking June and July.

REPRESENTATIVE SPECIMENS. **China.** YUNNAN: Yangtze-Mekong divide, Lopa and Shupa valleys, 28°N., *Forrest* 435 (E); E. flank of Tali Range, 25°40'N., *Forrest* 4184 (E); Mekong-Salwin divide, 28°12'N., *Forrest* 14986 (E, K); Shweli-Salwin divide, 25°30'N., 98°58'E., *Forrest* 24265 (E, NY, US, W); N' Maikha-Salwin divide, 26°20'N., *Forrest* 17999 (A, E, K); Ta-li, Mt. Tsang-chan, *Delavay* 1889 (A, F, P); Ta-li Hsien, *Wang* 63203 (A); Champutung, Shi-gi-tung, *Wang* 67121 (A); Salwin-Kiukiang divide, Newahlung, *Yü* 19302 (A); Taron-Taru divide, Bucalwang Valley, *Yü* 20085 (A, E). TIBET: Kongbo prov., Tum La, Nayu, 29°N., 94°E., *Ludlow et al.* 5804 (A, E). **Burma:** Hpiman Pass, *R. A.* 1069 (E); Shing-Hong Camp, *R. A.* 1642 (E); N'mai-Kha-Salwin divide, 26°25'N., *Forrest* 29656 (E); Kachin state, Sumprabum subdiv., E. approaches from Sumprabum to Kumon Range, Bumpha Bum, 26°40'N., 97°20'E., *Keenan et al.* 3538 (A, E); frontier of Tibet and Burma, Senighku Wang (Advance Base), *Ward* 6890 (K); Adung Valley 28°20'N., 97°45'E., *Ward* 9749 (A, in part); N. Triangle (Tama Bum), Kachin state, *Ward* 20998 (A, E).

4c. *Lyonia villosa* (Wallich ex Clark) Hand.-Mazz. var. **pubescens** (Franchet) Judd, comb. nov.

Pieris ovalifolia (Wallich) Drude var. *pubescens* Franchet, *Nouv. Arch. Mus. Paris*, sér. 2. 10: 44. 1887. *Pieris villosa* Wallich ex Clark var. *pubescens* (Franchet) Rehder & Wilson in *Sarg. Pl. Wilsonianae* 1: 554. 1913. *Xolisma villosa* (Wallich ex Clark) Rehder var. *pubescens* (Franchet) Rehder, *Jour. Arnold Arb.* 5: 53. 1924. TYPE: China, prov. Tibet oriental [actually Szechwan], Moupine [Poshin], "in regione maxime excelsa," Aug. 1869, *David s.n.* (not seen).

Deciduous low to erect shrub to 3.4(-4.5) meters tall. Twigs sparsely to densely pubescent. Buds glabrous to densely pubescent. Leaf blades (2.5-) 3-7(-8.5) by (1-)1.5-4(-5.5) cm.; apex acute to rounded with short (to ca. 4 mm.) mucro, or shortly acuminate; abaxial surface often smooth, at most obscurely papillose, very sparsely to densely pubescent along midvein (especially proximal portion) and often along many 2° (and occasionally even 3°) veins, or occasionally completely glabrous; petiole (2.5-)3-10 mm. long, pubescent adaxially or all around. Inflorescences 1-4(-6) cm. long. Pedicels moderately to densely crisped- or straight-pubescent. Calyx lobes (2-)3-5(-6.5) mm. long, abaxial surface glabrous to sparsely or densely pubescent; corolla cylindrical to less commonly urceolate, (4.5-)6.5-9(-11) by 3-4.5(-6) mm.; ovary glabrous to moderately pubescent. Capsule ovoid to globose, (2.5-)3-4.5 mm. long, glabrous to sparsely pubescent. (FIGURES 26, 27; see also Anonymous, 1974a.)

DISTRIBUTION AND ECOLOGY. Southeastern Tibet, extreme northern Burma, northern Yunnan, and southwestern Szechwan, with disjunct occurrence in Bhutan (MAP 8). *Pinus* forests, *Quercus-Ilex* forests, bamboo thickets, *Larix* and *Abies* forests, rocky openings in *Rhododendron* thickets, mixed temperate forests, dense thickets, forest margins, and rocky, scrub-clad slopes; (1800-) 2300-3800(-4100) m. alt. Flowering mainly late May through July.

REPRESENTATIVE SPECIMENS. **China.** SZECHWAN: Ta Hsieng Ling, Han Yueh, *Chiao* 1615 (A); Pao-hsing Hsien, *Chu* 3416 (A, E, K); Daliang-schan, E. of Ningyueh,

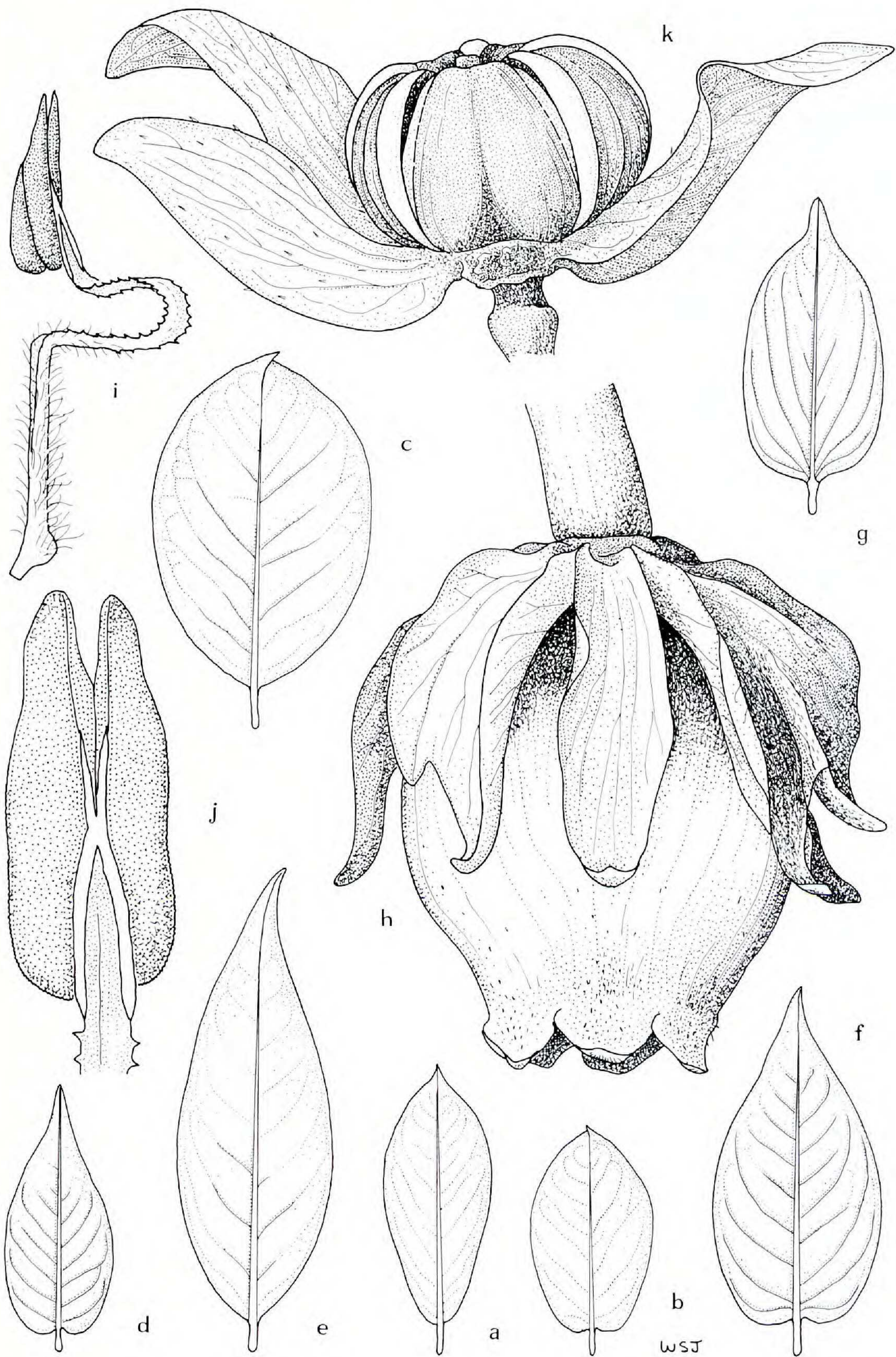


FIGURE 27. a-c, *Lyonia villosa* var. *pubescens* (in part), leaves, $\times .5$. d-k, *L. macrocalyx*: d-g, leaves, $\times .5$; h, flower, $\times 6$; i, stamen, $\times 12.5$; j, anther, $\times 25$; k, capsule, $\times 6$.

near Lanba, *Handel-Mazzetti* 1665 (w); Omei Hsien, Mt. Omei, *Hu* 8217 (us); Muli territory, between Baurong and Kulu, W. of Yalung R., *Rock* 17813 (A, E, NY, US); Muti Konka, snow range E. of Yalung R., *Rock* 23707 (A, E, K, NY, UC); prov. Batang, Yargong, *Soulie* 3633 (p); near Wen-chuan Hsien, Wa-sen country, *Wilson* 3191 (A); Wa-shan, *Wilson* 3192 (A, E, K, US); NE. of Tachien-lu, *Wilson* 4194 (A, E, K, US); Juei-she Hsien, *Yü* 1023 (A); Lei-po Hsien, *Yü* 3444 (E); Mu-li, Wa-chin, Wa-ti, *Yü* 14702 (A). YUNNAN: Tali, Chicken-foot Mt., *Chen* 2396 (E); NE. of Likiang, Tzai-koo Snow Mt., *Feng* 2531 (A); Mekong-Salwin divide, 28°12'N., *Forrest* 431 (E); E. flank of Lichiang Range, lat. 27°15'N., *Forrest* 2442 (E); Tsekou, *Monbeig s.n.*, 20 July 1912 (B, F); Wei-se Hsien, *Tsai* 59664 (A); Ta-li Hsien, *Wang* 63206 (A); Nar-jou, Tsa-wa-rung, *Wang* 66530 (A); A-tun-tze, Dokerla, *Yü* 7963 (A, E); Chung-tien, Hsiao chungtien, *Yü* 10957 (A); Wei-hsi, W. of Tungchuling, *Yü* 10730 (E). TIBET: Kongbo prov., Tamnyen La, 29°20'N., 94°43'E., *Ludlow et al.* 4925 (A, E); Pe, Tsangpo Valley, 29°31'N., 94°54'E., *Ludlow et al.* 5166 (A, E); Kongbo prov., Molo, 28°45'N., 90°E., *Ludlow et al.* 5660 (E); Lilung Chu, Tsangpo Valley, 20°N., 94°E., *Ludlow et al.* 5695 (E); Pome prov., Showa La, *Ludlow et al.* 13174 (A, E); Kongbo prov., Je, Pasum Tso, *Ludlow et al.* 14083 (E); Kongbo prov., Deyang La, *Ludlow et al.* 14301 (E). **Burma:** Adung Valley, *Ward* 9540 (A). **Bhutan:** between Laya and Gyasa Dzong, Mo Chu, *Ludlow et al.* 16480 (A, E).

Lyonia villosa is most closely related to the widespread and variable *L. ovalifolia*, which occurs chiefly at lower elevations (FIGURE 7). *Lyonia villosa* differs consistently from all varieties of *L. ovalifolia* in its lack of two spurs (or appendages) on the filament just below the anther-filament junction.

Populations of *Lyonia villosa* are separable into three morphologically distinct and geographically isolated varieties (MAP 8). These varieties are distinguished mainly by differences in the distribution of unicellular hairs, the size of the leaves, and the shape and size of the corollas (see key). As its name implies, *L. villosa* var. *pubescens* tends to have all its parts more densely covered with unicellular hairs than does either var. *villosa* or var. *sphaerantha*. Although it has been stated (for example, by Rehder, 1924) that this taxon can be differentiated from "typical" *L. villosa* by its pubescent ovary, this is often untrue. Some plants do, indeed, have unicellular hairs on the ovary, but others completely lack these hairs or have only a very few.

Of the three varieties of *Lyonia villosa*, var. *pubescens* is the most variable. Plants of this taxon collected from Bhutan and from extreme northern Burma, and some of those from southeastern Tibet, tend to have small leaves (to ca. 4.5 cm. long) that are quite wide in relation to their length, and small, urceolate to long-urceolate flowers. Such plants are superficially similar to *L. villosa* var. *sphaerantha* but can be easily separated by their moderate to dense covering of unicellular hairs on the pedicels and on the major veins (or at least the lower portion of the midvein) on the abaxial leaf surface. These forms intergrade completely with the more typical representatives of var. *pubescens* of Yunnan and Szechwan (i.e., plants with rather large leaves and more or less cylindrical flowers).

The ranges of *Lyonia villosa* vars. *sphaerantha* and *pubescens* overlap

in extreme northwestern Yunnan and adjacent Burma, where intermediate plants seem to be rather common (for example, see: Yunnan, Ta-li, *Delavay* 1889 (F, in part), Lo-pin-chan, Lan-kong, *Delavay* 4313 (A, US), Tsekou, *Soulier* 1357 (A, F, L), Sung-kwei Pass, Lang-kong Valley, 26°12'N., *Forrest* 5842 (E, K); Burma, Adung Valley, *Ward* 9749 (A, in part)). These unusual plants have both papillae and unicellular hairs on their abaxial leaf surfaces and often have quite pubescent pedicels; they tend to have leaves and flowers intermediate in shape and size and seem to be completely fertile.

Lyonia villosa vars. *pubescens* and *sphaerantha* have probably both occasionally hybridized with *L. ovalifolia*; these hybrids are discussed under the latter taxon. I have seen no specimens intermediate between *L. villosa* var. *villosa* and *L. ovalifolia*, although Osmaston (1927) said that he found the two growing together at 9500 ft. at the head of the Nandagini Valley in Kumaon (India).

5. *Lyonia macrocalyx* (Anthony) Airy Shaw, Curtis's Bot. Mag. **160**: t. 9490. 1937.

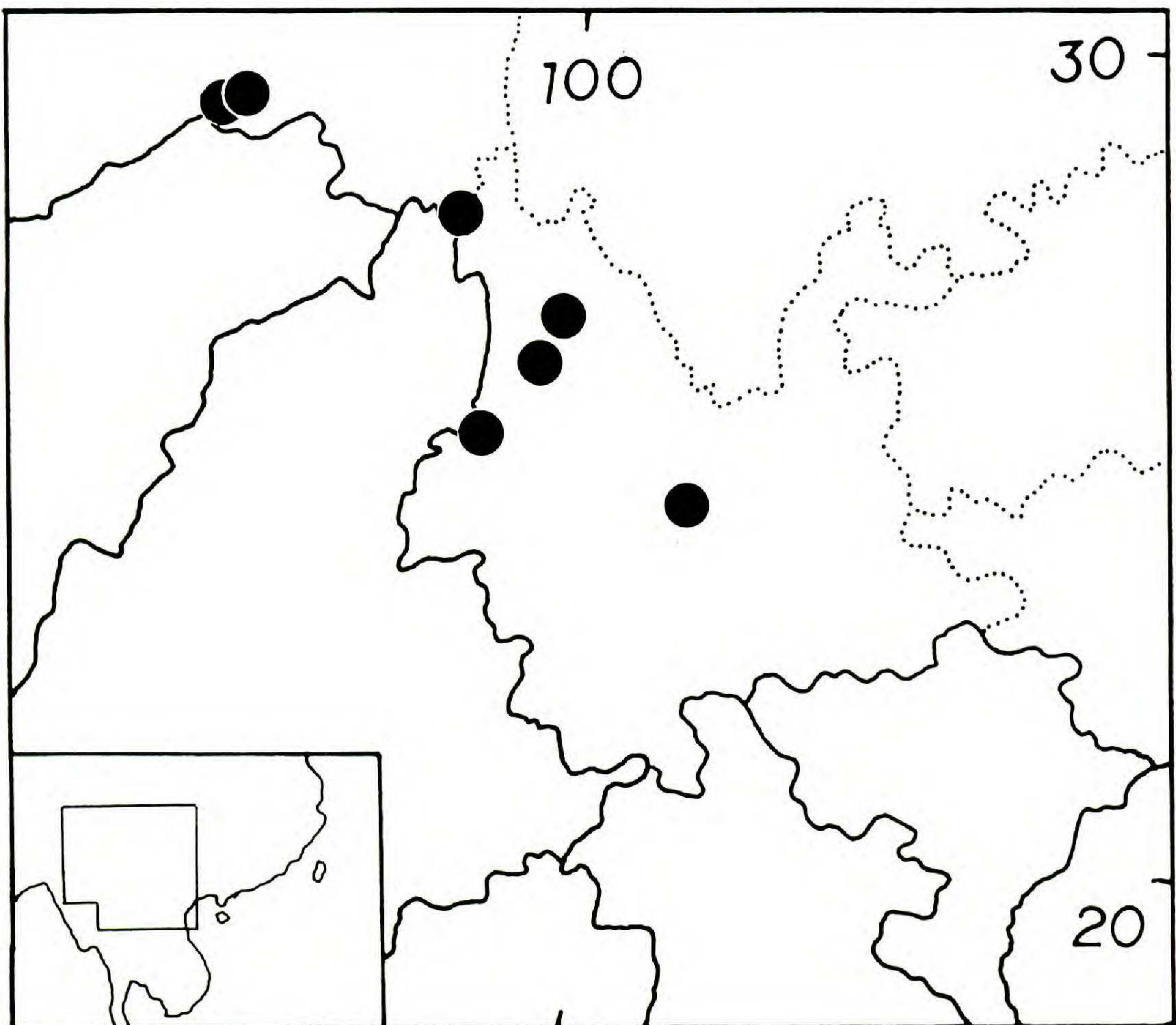
Pieris macrocalyx Anthony, Notes Roy. Bot. Gard. Edinburgh **15**: 241. 1927. TYPE: [China], prov. Yunnan, hills N. of Lung-fan, 25°54'N., 98°33'E., alt. 9000 ft., June 1925, *G. Forrest* 26800 (holotype, E!; isotypes, A!, P!, S!, US!).

Semi-evergreen to deciduous shrub to ca. 3 meters tall, with brownish to gray, longitudinally furrowed bark. Twigs terete to very slightly angled, slender, with few long-headed hairs, otherwise glabrous. Buds elongate-ovoid to ovoid, 1.5–10 by 1.5–4.5 mm. Leaf blades ovate to nearly elliptic, (3.5–)5–10.5(–13) by (1.5–)2.5–4(–5) cm., ± flat, slightly coriaceous, ca. 0.17–0.24 mm. thick; apex acuminate to long-acuminate; base ± broadly cuneate to slightly cordate; margin entire, plane to slightly revolute; venation eucamptodromous (rarely acrodromous, imperfect, suprabasal) to brochidodromous, 3° veins reticulate to percurrent; adaxial surface with sparse long-headed hairs, sparsely pubescent on midvein, otherwise glabrescent, with 3° and higher order veins obscure to visible, and 2° veins often slightly depressed; abaxial surface strongly papillose, glaucous, with long-headed hairs, otherwise glabrous, with 3° and higher order veins slightly and laxly reticulate, and 2° veins raised and visible, smoothly arching toward margin, or sinuous and ± irregular; petiole 2.5–10 mm. long, with long-headed hairs, otherwise glabrous or pubescent adaxially. Flower buds usually below vegetative buds; inflorescences racemose, to ca. 10-flowered, 0.5–5.5(–6.5) cm. long, slightly ascending; flowers pendulous and secund. Pedicels slender to moderately stout, 5–11 mm. long, often with long-headed hairs, otherwise glabrous; bracteoles opposite, basal, ovate, 1.5–6 mm. long; bracts 0.8–3 cm. long, 1 to 3 near base of raceme usually large and leaflike, the others small, similar to bracteoles, usually caducous. Flowers 5-merous, but calyx often variable; calyx lobes 5 (to 8) (due to partial and/or complete division of 1 or more lobes into a compound structure), persistent to occasionally deciduous, triangular to ovate, with acute or obtuse to acuminate apices, 4.5–9(–11)

by 1.5–5.5(–7) mm., the adaxial side usually with few long-headed hairs, otherwise glabrous, the abaxial side papillose and glaucous, with scattered long-headed hairs, otherwise glabrous; corolla urceolate to globose, 6.5–9 by 5–6.5 mm., white, abaxially with sparse long-headed hairs; filaments moderately to densely long-pubescent, especially near base, 4.5–6 mm. long, unappendaged, anthers 1.5–2 mm. long; ovary glabrous, placentae \pm subapical. Capsule \pm subglobose, 3–4.5 by 4–6 mm., glabrous, with pale, strongly thickened sutures that in dehiscence usually split irregularly and remain attached to an adjacent valve; seeds 0.7–1.5 mm. long. (FIGURE 27; see also Airy Shaw (1937), Stevens (1970).)

DISTRIBUTION AND ECOLOGY. China, chiefly northwestern portions of Yunnan and southeastern parts of Tibet, probably also in northern Burma (MAP 9). Mountainous areas, forests, open scrub vegetation of rocky slopes; ca. 1900–3300 m. alt. Flowering chiefly May to July.

REPRESENTATIVE SPECIMENS. **China.** TIBET: Trulung, Po Tsangpo, Pome, *Ludlow et al.* 13029 (E); Tsangpo Gorge, *Ward* 6317 (E, K); Taron-Taru divide, Lungnan to Tehgai, *Yü* 20885 (A, E). YUNNAN: Salwin-Kui-chiang divide, 27°15'N., 98°40'E., *Forrest* 25567 (E, K, US, W); N. of Lung-fan, 25°54'N., 98°33'E.,



MAP 9. Distribution of *Lyonia macrocalyx* (Yunnan and Tibet).

Forrest 27741 (A, E, W); Shang-pa Hsien, *Tsai 54886* (A); Laktang, *Ward 3226* (E).

Lyonia macrocalyx, a distinctive and beautiful plant, can easily be recognized by its subfoliaceous, elongate, and usually greatly expanded calyx lobes; its large, urceolate corollas; its unappendaged filaments; and its coriaceous, semi-evergreen leaves with the apex long-acuminate, the major veins on the adaxial surface often slightly depressed, and the abaxial surface papillose and glaucous. It is readily distinguished from its nearest allies, *L. villosa* and the variable *L. ovalifolia*, by the characters given above. Although these three taxa have overlapping geographic ranges, it is not known whether they ever occur together.

Occasionally the secondary veins arising from near the base of the leaf blade are so strongly developed that a nearly plinerved condition occurs.

Lyonia Nutt. sect. *ARSENOCOCCUS* (Small) Judd, comb. nov.

Arsenococcus Small in Small & Carter, Fl. Lancaster Co. 218. 1913. *Xolisma* Raf. sect. *Arsenococcus* (Small) Rehder, Jour. Arnold Arb. 5: 54. 1924.
TYPE SPECIES: *Lyonia ligustrina* (L.) DC.

Deciduous shrubs, often spreading by horizontal underground rhizomes, the branches with heterogeneous pith. Indumentum of unicellular hairs and multicellular, biseriate-stalked, extremely long-headed hairs. Buds with 2 large, imbricate scales. Leaves serrulate, with unlignified or only slightly lignified epidermis, lacking hypodermis. Flowers usually 5-merous, in small panicles; calyx lobes valvate in bud; corolla urceolate; filaments with \pm long, unicellular hairs near base, with pair of small spurs below junction with anthers; placentae positioned subapically on columella. Capsules with pale, \pm moderately thickened sutures, usually adhering to valve or splitting irregularly in dehiscence; seeds oblong-ovoid to spindle shaped, ends sometimes truncated.

DISTRIBUTION. United States: Coastal Plain, Piedmont, and mountains; Maine, south to Florida, west to eastern Texas, Arkansas, and Oklahoma.

NUMBER OF SPECIES (TAXA). 1 (2).

6. *Lyonia ligustrina* (L.) DC. Prodr. 7: 599. 1839.

Deciduous to semi-evergreen shrub to ca. 4 meters tall, with grayish, shallowly and longitudinally furrowed bark; often spreading vegetatively by horizontal underground rhizomes. Twigs terete to slightly angled, slender, sometimes turning reddish in autumn, with scattered long-headed hairs, otherwise glabrous to densely pubescent. Buds elongate-ovoid, 1-4 by 0.5-1.8 mm., often red in autumn. Leaf blades narrowly to widely elliptic, obovate, or ovate, (1.5-)2-9.5(-10.5) by 1-4.5(-5) cm., \pm flat, chartaceous to slightly coriaceous, ca. 0.15-0.26 mm. thick, often turning reddish in autumn; apex acute to acuminate or mucronate; base attenuate, narrowly to broadly cuneate or rounded; margin clearly to minutely serrulate, plane to slightly revolute; venation brochidodromous, with 3° veins reticulate to \pm percurrent; adaxial

surface with sparse to dense long-headed hairs (these sometimes deciduous with age), sparsely to densely pubescent on midvein, especially proximal portion, and sometimes also on 2° veins, with 3° and higher order veins obscure to slightly visible, and 2° veins usually not depressed; abaxial surface with sparse to dense long-headed hairs, otherwise glabrous to densely pubescent on midvein and sometimes on 2° (or even 3°) veins, the 3° and higher order veins obscure to slightly visible and 2° veins slightly to strongly raised, sinuous to straight or slightly curved toward apex; petiole 1–8 mm. long, with long-headed hairs, otherwise pubescent adaxially or all around. Flower buds usually above vegetative buds; inflorescences racemes of fascicles to racemes of short racemes, to 15- to 45- (to 60-)flowered, 0.5–6(–9) cm. long, horizontal to slightly ascending. Pedicels usually slender, (1–)2–10 mm. long, with long-headed hairs, otherwise glabrous to densely pubescent; bracteoles opposite, basal, triangular to linear, 0.2–1.3 mm. long, often caducous; bracts all very small and similar to bracteoles in shape, or with very few to many large and leaflike, to 3 cm. long, and others small and caducous. Flowers usually 5-merous; calyx lobes triangular, with acuminate apices, 0.5–1.5 by 0.4–1 mm., the adaxial side glabrous, the abaxial side with scattered long-headed hairs, otherwise glabrous to densely pubescent; corolla urceolate, 2–4(–4.5) by 2–4.5 mm., white, abaxially with sparse to dense long-headed hairs, rarely also sparsely pubescent; filaments with long-unicellular hairs near base, 1–2 mm. long, with 2 short spurs below anther-filament junction, anthers 0.6–1.2 mm. long; ovary densely covered with long-headed hairs, often otherwise pubescent, placentae ± subapical. Capsules globose to subglobose, 2–3 by 2–4 mm., usually with sparse to dense long-headed hairs, otherwise glabrous to moderately pubescent, with pale, much-thickened sutures that in dehiscence remain attached to an adjacent valve; seeds 0.7–1.7 mm. long.

DISTRIBUTION. United States (Maine to Florida, west to Arkansas, Texas, and Oklahoma); various habitats of mountains, Piedmont, and Coastal Plain; near sea level to nearly 2000 m. alt.

COMMON NAMES. Maleberry, he-huckleberry, male-huckleberry, male-blueberry, seedy-buckberry.

Key to Varieties of *Lyonia ligustrina*

1. Inflorescences naked or with only few foliaceous bracts, [mountains and Piedmont south of Virginia; mountains, Piedmont, and Coastal Plain north of Virginia]. 6a. var. *ligustrina*.
1. Inflorescences with conspicuously foliaceous bracts or at least lower inflorescences with large bracts, [Coastal Plain from southeastern Virginia to Florida, west to eastern Texas, Oklahoma, and Arkansas (mountains)]. 6b. var. *foliosiflora*.

6a. *Lyonia ligustrina* (L.) DC. var. *ligustrina*

Vaccinium ligustrinum L. Sp. Pl. 351. 1753. *Andromeda ligustrina* (L.) Muhl. Catal. Pl. Am. Sept. 44. 1813. *Xolisma ligustrina* (L.) Britton, Mem. Torrey Bot. Club 4: 135. 1894. *Arsenococcus ligustrinus* (L.) Small

in Small & Carter, Fl. Lancaster Co. 218. 1913. *Lyonia ligustrina* (L.) DC. var. *typica* Fern. *Rhodora* 43: 625. 1941. TYPE: "in Pennsylvania," *Kalm s.n.* (lectotype, LINN, sheet no. 497.11, microfiche photo seen).

Andromeda paniculata L. var. *nudiflora* Michaux, Fl. Bor. Am. 1: 255. 1803. TYPE: Pennsylvania, *A. Michaux s.n.* (lectotype, P-MICHX (IDC 6211. 58: I. 7!)).

Deciduous shrub. Buds glabrous to sparsely pubescent. Leaf blade \pm chartaceous. Pedicels (1-)2-7.5 mm. long; bracts all very small and similar to the bracteoles (occasionally very few larger and leaflike, to 0.5-1.5(-2) cm. long), often quickly deciduous; inflorescences not conspicuously leafy. Corolla 2-4(-4.5) by 2-4.5 mm. (FIGURE 28; see also Watson (1825, t. 37., as *L. paniculata*); Britton & Brown (1913); Gleason (1952); Graves (1952); Braun (1961); Radford, Ahles, & Bell (1968); Campbell & Hyland (1975, pl. XLVIII, 2.)

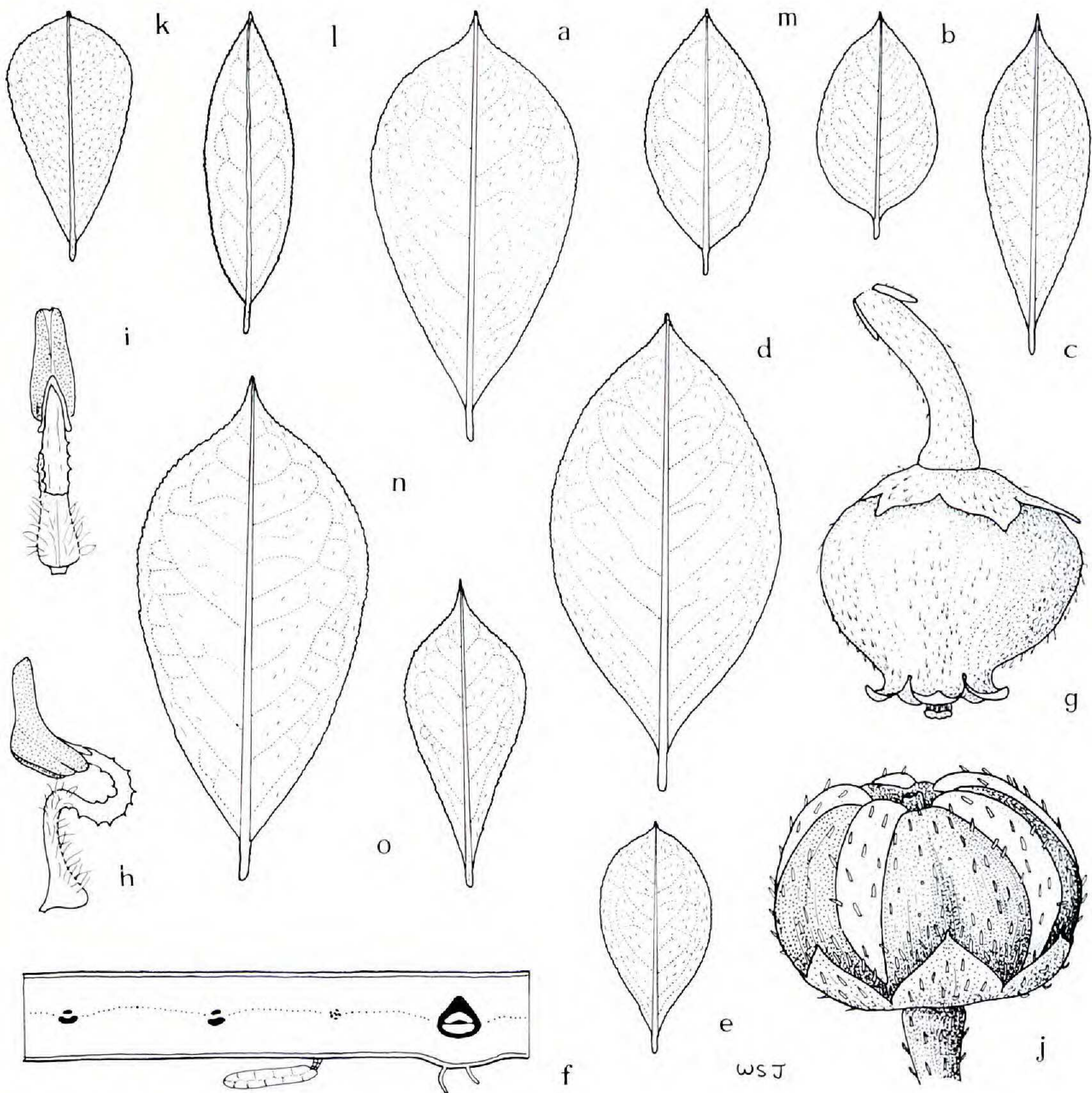
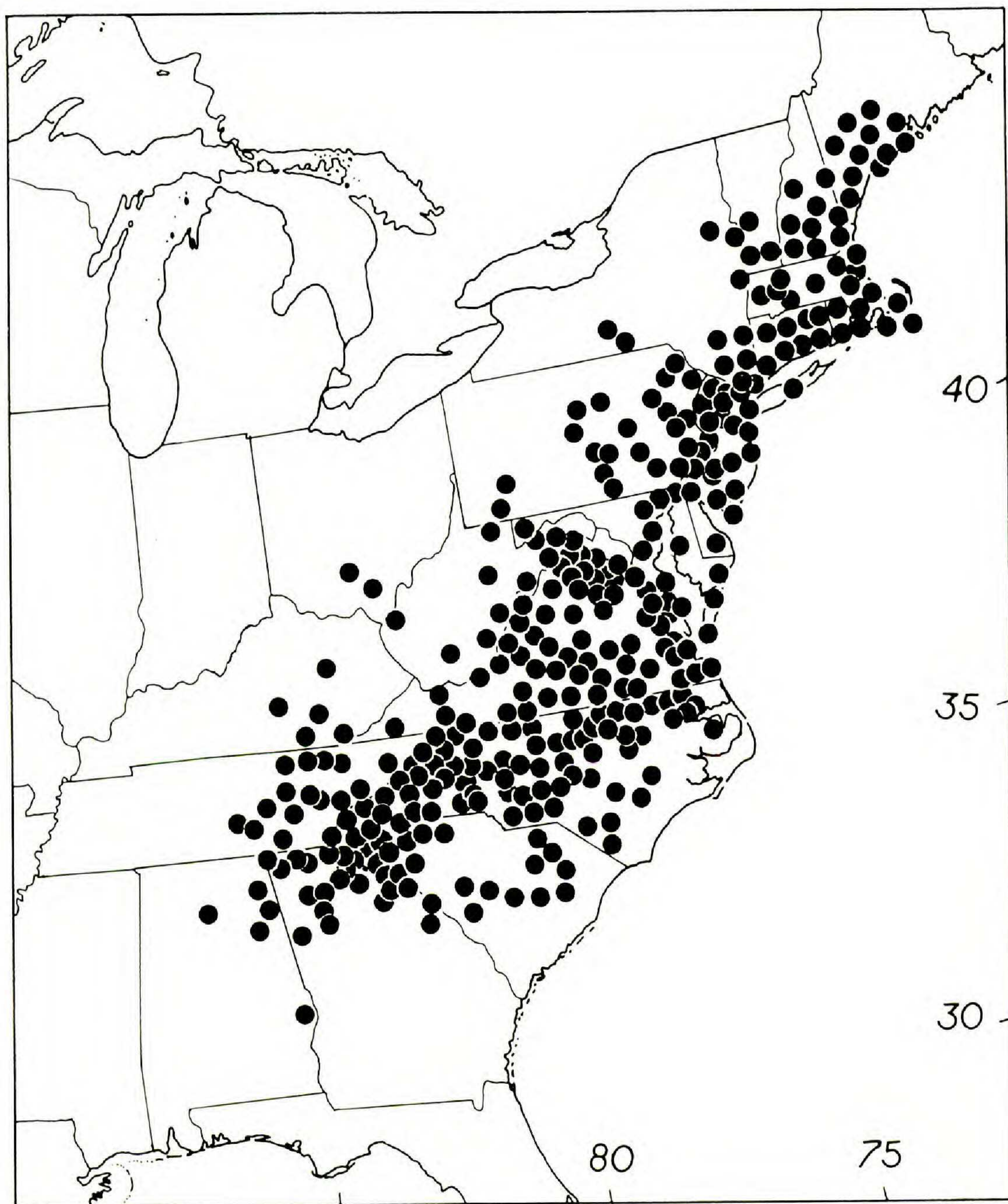


FIGURE 28. a-j, *Lyonia ligustrina* var. *ligustrina*: a-e, leaves, $\times .5$; f, cross section of leaf blade, $\times 50$; g, flower, $\times 6$; h, i, stamens, $\times 12.5$; j, capsule, $\times 6$. k-o, *L. ligustrina* var. *foliosiflora*, leaves, $\times .5$.

DISTRIBUTION AND ECOLOGY. United States (South Carolina, northern Georgia and Alabama, to Maine); mountains, Piedmont, and Coastal Plain (MAP 10). Moist to dry acid woods and thickets, forest-, pond-, swamp-, or river-margins, grassy and/or heath balds, acid swamps and bogs; sea level to nearly 2000 m. alt. Especially prevalent in *Acer rubrum* swamps, *Pinus* and/or *Quercus* woods, and thickets of *Vaccinium*, *Rhododendron*, or other ericads. Flowering late April through early July, varying greatly with latitude and elevation.

REPRESENTATIVE SPECIMENS. United States. MAINE. KNOX Co.: S. shore of Newbert Pond, Appleton, *Rossbach 1557* (NCU). Oxford Co.: Lovell, *Johnson 111* (NY).



MAP 10. Distribution of *Lyonia ligustrina* var. *ligustrina*.

Somerset Co.: near Pittsfield, *Knight 1840* (GH). York Co.: 0.75 mi. N. of Bauneg Beg Pond, *True 5147* (GH). NEW HAMPSHIRE. Cheshire Co.: near E. Jaffrey, *Palmer 43033* (A). Grafton Co.: E. Hebron, *Nelson s.n.*, 10 July 1917 (NY). Merrimack Co.: Hooksett, *Batchelder s.n.*, 16 July 1921 (NEBC). Rockingham Co.: Fox Hill Point, N. Hampton, *Harris 20991* (NEBC). VERMONT. Bennington Co.: Pownal, *Eggleston 1424* (NY). Rutland Co.: Tadmire Hill, Pawlet, *Dutton 1175* (A). MASSACHUSETTS. Barnstable Co.: near Orleans, *Palmer 44807* (GH). Berkshire Co.: Mt. Washington, *Moldenke 11651* (NY). Middlesex Co.: near Long Bridge, Newton, *Gilbert s.n.*, 19 June 1894 (GH). Nantucket Co.: Polpis, Nantucket Is., *MacKeever N532* (NY). Worcester Co.: Pine Hill, Lancaster, *Brown s.n.*, 20 August 1942 (TEX). RHODE ISLAND. Newport Co.: Newport, *Mearns 611* (NY). Providence Co.: near Harrisville, *Palmer 44967* (A). CONNECTICUT. Fairfield Co.: near New Canaan, *Harger 7684* (GH). Hartford Co.: Southington, *Andrews s.n.*, 26 August 1903 (GH). New London Co.: near Stonington, *Harger 6310* (NCU). NEW YORK. Dutchess Co.: near Clove, *Standley & Bollman 11908* (US). Orange Co.: Black Rock Forest, *Raup 7805* (GH). Rensselaer Co.: Sandlake, *House 5181* (NY). Suffolk Co.: Hauppauge Bog, Cold Spring Harbor, *Cain 484* (NY). Tompkins Co.: South Hill, Ithaca, *Eames & Thomas 4770* (GH). Warren Co.: 2 mi. S. of Luzerne, *Fogg 19209* (NY). PENNSYLVANIA. Adams Co.: 5.75 mi. WSW. of Wenksville, *Tanger 4381* (DUKE). Bucks Co.: 2.5 mi. NW. of Neshaminy, *McDowell 395* (GH). Centre Co.: 1 mi. W. of Hublersburg, *Wahl 520* (GH). Fayette Co.: Ohio-pyle, *Bright 16920* (TEX). Juniata Co.: Tuscarora Mt., 3.5 mi. S. of Port Royal, *Adams 5237* (A). Luzerne Co.: along Susquehanna R. above Nescopec, *Heller 14215* (A). NEW JERSEY. Bergen Co.: Franklin Lakes, *Moldenke 10745* (NY). Cape May Co.: 2 mi. SE. of Goshen, *Lems s.n.*, June 1962 (MSC). Gloucester Co.: Riders Bog, near Nialaga, *Bassett s.n.*, 23 August 1923 (GH). Ocean Co.: 2 mi. E. of Cedar Grove, *Fogg 4849* (GH). Sussex Co.: 1-2 mi. N. of Sparta, *Adams & Wherry 1541* (A). DELAWARE. New Castle Co.: Highland Woods off Darley Rd., *Reed 51105* (MSC). Sussex Co.: 4 mi. W. of Rehoboth Beach, near Love Creek, *McVaugh 6545* (GH, NY). DISTRICT OF COLUMBIA: Takoma Park, *Painter 304* (DUKE). MARYLAND. Charles Co.: Wolfden Creek, Cedarville State Forest, *Simpson s.n.*, 5 July 1952 (US). Garrett Co.: Mt. Lake Park, *Shreve 540* (US). Hartford Co.: 0.5 mi. SSW. of Havre de Grace, *Shull 157* (NY). Talbot Co.: Miles Creek, 2 mi. NE. of Trappe, *Earle 1693* (GH). Worcester Co.: along edge of Corker's Creek, 4 mi. S. of Snow Hill, *Judd 33* (MSC). VIRGINIA. Albemarle Co.: at Albemarle-Nelson county line on Va. 6, *James 12136* (NCU). Fauquier Co.: 3 mi. below Thorofare Gap, Pond Mt., *Allard 11329* (GH). Isle of Wight Co.: near Franklin, *Heller s.n.*, 7-28 June 1893 (A). King William Co.: banks of Mattaponi R. near King William Landing, *Fernald & Long 11601* (GH, NY). Mecklenburg Co.: E. of Boydton, *Gleason 8690* (NY). Pittsylvania Co.: NE. of Kentuck, *James 3192* (NCU). Pulaski Co.: NW. of Pulaski, *James 8509* (NCU). Rockingham Co.: above Hone Quarry Camp, *Allard 2114* (US). Scott Co.: 2.5 mi. E. of jct. of U.S. 58 and Co. Rd. 701, *James 9660* (NCU). WEST VIRGINIA. Cabell Co.: Rickett's Place, *Gilbert 556* (FSU, DUKE, GH, NY, US). Greenbrier Co.: White Sulphur Springs, *Hunnewell 6747* (GH). Hampshire Co.: Campon Springs, *Hunnewell 17984* (GH). Pendleton Co.: Shenandoah Mt., near U.S. 33, *Radford 45912* (NCU). Upshur Co.: Buckhannon, *Millspaugh 411* (NY). NORTH CAROLINA. Alamance Co.: 18.7 mi. W. of Chapel Hill, *Radford & Rabb 714* (NCU). Ashe Co.: 4 mi. NE. of Jefferson, *Radford 6233* (NCU). Buncombe Co.: near Biltmore, *Biltmore Herbarium 26* (GH, NCU, NY). Cherokee Co.: 1 mi. SE.

of Unaka, *Radford* 17591 (NCU). Duplin Co.: 5.5 mi. N. of Beulaville, *Ahles* 24084 (NCU). Iredell Co.: 4 mi. ENE. of Harmony, *Ahles* 45222 (NCU). Macon Co.: N. of Highlands, *Godfrey* 51465 (FSU). Northampton Co.: 2.1 mi. WNW. of Garysburg, *Ahles* 45592 (NCU). Richmond Co.: along Drowning Creek, on U.S. 1 just S. of Moore Co. line, *Fox* 3671 (GH). Wake Co.: Lake Johnson, *Godfrey* 49403 (GH). SOUTH CAROLINA. Aiken Co.: 1.3 mi. W. of jct. of U.S. I-76 and S.C. 254, *Ahles* 55471 (NCU). Clarendon Co.: 3 mi. SW. of Manning, *Godfrey & Tryon* 906a (GH, NY). Florence Co.: 1.8 mi. WSW. of Hyman, *Bell* 7563 (NCU). Greenville Co.: above River Falls, *Rodgers & Mullens* 67211 (NCU). Oconee Co.: 7 mi. NW. of Jocassee, *Radford* 17725 (NCU). Spartanburg Co.: N. of Spartanburg, *Bell* 8343 (NCU). GEORGIA. Bartow Co.: 4.5 mi. SE. of Adairsville, *Greear* 64417 (GA, NCU). Carroll Co.: 8.5 mi. N. of Carrolton, *Carnes* 66 (GA). Clarke Co.: near Athens, *Harper* s.n., 2 June 1897 (NY). Dade Co.: summit of Lookout Mt., *McVaugh* 9043 (NCU, TEX). Madison Co.: ca. 6 mi. from Ida, *Montgomery* 445 (GA). McDuffie Co.: near Thomson, *Bartlett* 1653 (NCU, VDB). Rabun Co.: Tallulah Falls, *Perry & Straham* 976 (NY). Whitfield Co.: Taylor's Ridge, *Wilson* 152 (NY). OHIO. Ross Co.: Liberty Twp., near Jones' Crossing, *Bartley & Pontius* 92 (NY). KENTUCKY. Bell Co.: near Middlesboro, *Gleason* 8828 (NY). Laurel Co.: near Corbin, *Horse* 2265 (GH). McCreary Co.: S. fork of Cumberland R., *Braun* 1016 (US). Powell Co.: Stanton, *McFarland* 2398 (US). TENNESSEE. Blount Co.: top of Gregory's Bald, *Wilson* 1783 (GH). Campbell Co.: near Pioneer, *Sharp et al.* 3828 (NCU). Carter Co.: near Roan Mt., *Rehder* s.n., 20 June 1900 (A). Coffee Co.: Manchester, *Godfrey* 69807 (FSU, NCU). Cumberland Co.: W. of Crossville, *Kral* 40544 (VDB). Hamilton Co.: Walden Ridge, above Soddy, *Underwood & Sharp* 2357 (NCU). Van Buren Co.: near Piney Creek Falls, *Shanks et al.* 4505 (NCU). ALABAMA. Calhoun Co.: 9.1 mi. NNE. of Jacksonville, *Clark* 16039 (NCU). Cherokee Co.: Little River Canyon Park, *Kral* 33351 (FSU, VDB). DeKalb Co.: DeSoto State Park, near Ft. Payne, *Kral* 36502 (VDB). Russell Co.: ca. 2 mi. W. of Phenix City, *Duncan* 9636 (GA, MO).

6b. *Lyonia ligustrina* (L.) DC. var. *foliosiflora* (Michaux) Fern. *Rhodora* 10: 53. 1908.

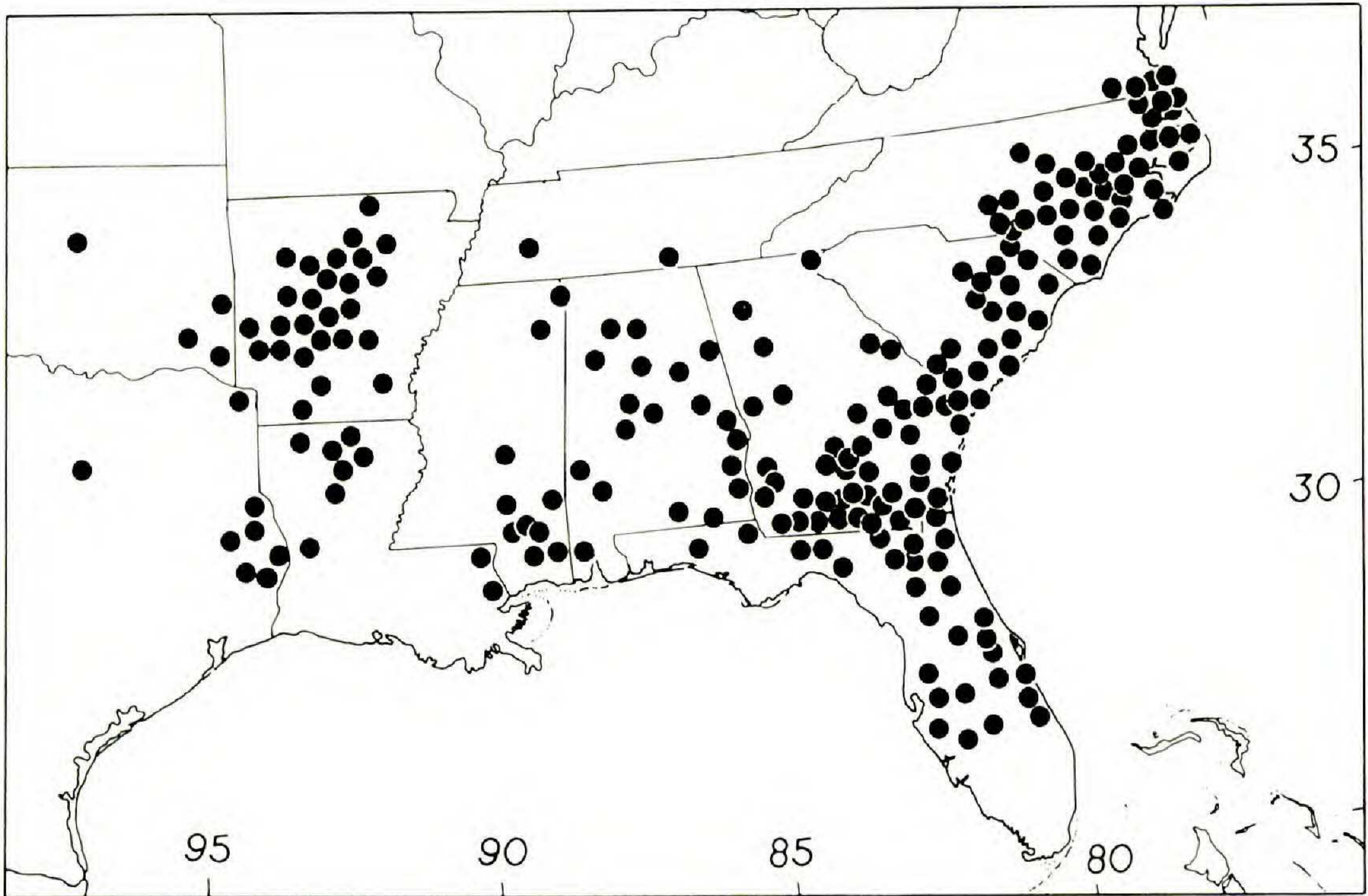
Andromeda paniculata L. var. *foliosiflora* Michaux, *Fl. Bor. Am.* 1: 255. 1803. *Andromeda frondosa* Pursh, *Fl. Am. Sept.* 295. 1814, *nomen novum*. *Lyonia frondosa* (Pursh) Nutt. *Gen. N. Am. Pl.* 1: 267. 1818. *Andromeda ligustrina* (L.) Muhl. var. *frondosa* (Pursh) Wood, *Class Book*, 488. 1861. *Andromeda ligustrina* (L.) Muhl. var. *pubescens* Gray, *Synopt. Fl. N. Am.* 2: 33. 1878, *nomen superfluum*. *Andromeda paniculata* L. var. *pubescens* (Gray) Dippel, *Handb. Laubholz.* 1: 370. 1889. *Xolisma ligustrina* (L.) Britton var. *foliosiflora* (Michaux) Mohr, *Bull. Torrey Bot. Club* 24: 24. 1897. *Xolisma foliosiflora* (Michaux) Small, *Fl. SE. U.S.* 889. 1903. *Andromeda ligustrina* (L.) Muhl. var. *foliosiflora* (Michaux) Fern. in Robinson & Fern. *Gray's Man.* ed. 7. 635. 1908. *Xolisma ligustrina* (L.) Britton var. *pubescens* (Gray) Millsp. *Liv. Fl. W. Virginia* 324. 1913. *Arsenococcus frondosus* (Pursh) Small, *Shrubs Florida*, 97. 1913. *Lyonia ligustrina* (L.) DC. var. *pubescens* (Gray) Bean, *Trees Shrubs Brit. Isles* 2: 64. 1914. (*Lyonia ligustrina pubescens* Rehder in Bailey, *Cycl. Am. Hort.* 1: 62. 1900, without citation of basionym or designation of rank). TYPE: United States, "in stagnosis," *A. Michaux* s.n. (lectotype, P-MICHX (IDC 6211. 58: II. 2!); duplicate of lectotype?, P!).

- Andromeda parabolica* Veillard in Duhamel, *Traité Arbres Arbustes*, ed. 2 (Nouv. Duhamel). 191. [1800–] 1801–1819 (but this description probably published ca. 1803). *Lyonia parabolica* (Veillard) Koch, *Dendrol.* 2: 199. 1872. TYPE: “l’Amérique septentrionale, dans la Georgie et la Floride” (not seen).
- Andromeda tomentosa* Dum.-Cours. *Bot. Cult.* ed. 2. 3: 495. 1811. *Andromeda paniculata* L. var. *tomentosa* (Dum.-Cours.) Dippel, *Handb. Laubholz.* 1: 369. 1889. TYPE: (not seen).
- Lyonia salicifolia* Watson, *Dendr. Brit.* 1: t. 38. 1825. *Lyonia ligustrina* (L.) DC. var. *salicifolia* (Watson) DC. *Prodr.* 7: 600. 1839. *Andromeda watsoniana* Steudel, *Nomencl. Bot.* ed. 2. 1: 89. 1840, *nomen novum*. TYPE: “Place . . . Arboretum, Kew. Country . . . North America” (not seen).
- Lyonia capreifolia* Watson, *Dendr. Brit.* 2: t. 127. 1825. *Lyonia ligustrina* (L.) DC. var. *capreifolia* (Watson) DC. *Prodr.* 7: 600. 1839. TYPE: “Place . . . Mr. James Lee’s, Hammersmith. Country . . . North America” (not seen).
- Lyonia multiflora* Watson, *Dendr. Brit.* 2: t. 128. 1825. *Andromeda polyantha* Steudel, *Nomencl. Bot.* ed. 2. 1: 89. 1840, *nomen novum*. TYPE: “Place . . . Mr. James Lee’s, Hammersmith. Country . . . North America” (not seen).
- Lyonia ligustrina* (L.) DC. f. *nanella* Fern. *Rhodora* 163: 158. 1947. TYPE: United States, Virginia, Nansemond Co., sphagnous and peaty bog by Norfolk and Western Railway about 0.5 mi. W. of Kilby, 8 and 12 Sept. 1946, *Fernald, Long, & Clement 15331* (holotype, GH!; isotype, US!).

Deciduous to semi-evergreen shrub. Buds glabrous to densely pubescent. Leaf blades \pm chartaceous to slightly coriaceous. Pedicels 2.5–10 mm. long; bracts variable, many large and leaflike, to 0.5–3 cm. long, others small and similar to bracteoles, sometimes quickly deciduous; inflorescences conspicuously leafy, or at least lower inflorescences with large bracts. Corolla 2–3.5 by 2–4 mm. (FIGURE 28; see also Watson (1825, t. 38 as *L. salicifolia*, t. 127 as *L. capreifolia*, t. 128 as *L. multiflora*); Vines (1960); and D. S. & H. B. Correll (1972).)

DISTRIBUTION AND ECOLOGY. United States, Atlantic Coastal Plain from southeastern Virginia to Florida, west to Arkansas, eastern Texas, and southeastern Oklahoma (MAP 11). Moist pine forests or flatwoods, acid thickets, shrub-bogs, marshy areas, stream-, pond-, or swamp-margins, *Taxodium* or *Chamaecyparis* swamps, swamps dominated by various broadleaved trees; near sea level to ca. 300 m. alt. Flowering late April through early July.

REPRESENTATIVE SPECIMENS. **United States.** VIRGINIA. Chesapeake Co.: Lake Drummond, Great Dismal Swamp, W. of Wallaceton, *Fernald & Long 13411* (GH). Nansemond Co.: E. of Cox Landing, *Fernald & Long 10765* (DUKE, GH). Southampton Co.: ca. 7 mi. S. of Franklin, *Fernald & Long 10006* (GH). NORTH CAROLINA. Beaufort Co.: 0.5 mi. N. of Wilmar, *Fox 4954* (NY). Bladen Co.: S. of Garland, *Blomquist s.n.*, 9 May 1951 (DUKE). Brunswick Co.: 7 mi. N. of Southport, *Wilbur 6715* (DUKE, TEX). Camden Co.: 1.3 mi. SW. of South Mills, *Lems s.n.*, 23 May 1959 (MSC). Carteret Co.: Harker’s



MAP 11. Distribution of *Lyonia ligustrina* var. *foliosiflora*.

Is., *Smith s.n.*, 10 May 1942 (NCU). Dare Co.: U.S. 264 near Mann's Harbor, *Radford 8196* (NCU). Harnett Co.: 1 mi. SE. of Pineview, *Wilbur 9110* (DUKE). Onslow Co.: 3.7 mi. WSW. of Haw, *Ahles 28174* (NCU). Orange Co.: 12 mi. NW. of Chapel Hill, *Wiegand & Manning 2393* (GH). SOUTH CAROLINA. Berkeley Co.: 8 mi. SW. of Monock's Corners, *Godfrey & Tryon 1405* (GH). Darlington Co.: Hartsville, *Smith s.n.*, 10 June 1942 (NCU). Florence Co.: 3 mi. W. of Cowards, *Bell 10864* (NCU). Horry Co.: Myrtle Beach, *Coker s.n.*, 12 July 1945 (NCU). Jasper Co.: Ridgeland, *Ahles 12306* (NCU). GEORGIA. Bartow Co.: 4.5 mi. SE. of Adairsville, *Greear 63104* (GA). Berrien Co.: W. of Ray City, *Bozeman 4748* (NCU). Charlton Co.: W. of Chessar's Is., Okefenokee Swamp, *Duncan 2007* (NY). Chatham Co.: Savannah, *Nuttall s.n.* (GH). Decatur Co.: 3 mi. W. of Faceville, *Thorne 4792* (NY). Lowndes Co.: 10 mi. ESE. of Valdosta, *Faircloth 4767* (NCU). McIntosh Co.: 1.3 mi. NE. of Ft. Barrington, *Bozeman 2354* (NCU). Screven Co.: near Cameron, *Reade E1625* (GA). Telfair Co.: 3 mi. NW. of Lumber City, *Wilbur 3152* (GA). FLORIDA. Alachua Co.: near Devil's Millhopper, *Wiggins 19754* (NCU, FLAS). Jefferson Co.: near Lloyd, *Godfrey 61426* (FSU). Hamilton Co.: 6 mi. E. of Jasper, *Godfrey 58511* (FSU, GH, VDB). Highlands Co.: Sebring, *Harbison 17* (A, NCU). Jackson Co.: 5 mi. E. of Marianna, *Hood & West 2022* (FLAS). Lake Co.: near Eustis, *Nash 528* (A, MSC, US). Nassau Co.: 6 mi. S. of Callahan, *Will & Ward s.n.*, 17 June 1961 (FLAS). Seminole Co.: N. of Goldenrod, *Cooley et al. 7404* (NCU). TENNESSEE. Franklin Co.: near Tallahoma, *Alexander et al. s.n.*, 24 Sept. 1933 (NY). Madison Co.: Jackson, *Bain 426* (NY). ALABAMA. Chilton Co.: 6.6 mi. NE. of Clanton, *Clark 17637* (NCU). Clark Co.: 6 mi. S. of Thomasville School, *Kral 41107* (VDB). Covington Co.: 17 mi. SSE. of Andalusia, *Duncan 15013* (NCU). Cullman Co.: St. Bernard, *Wolf s.n.*, 29 May 1922 (NCU). Henry Co.: 8 mi. N. of Headland, *Wiegand & Manning*

2396 (GH). Mobile Co.: near Mobile, *Mohr s.n.*, 13 May 1893 (A). Talladega Co.: along Salt Creek, T. 16 S., R. 8 E., *Clark 2844* (NCU). Winston Co.: Camp McDowell, along Clear Creek, *Clark 12969* (NCU). MISSISSIPPI. Covington Co.: S. of Hot Coffee, *Jones 2859* (GA). Forrest Co.: Hattiesburg, *Jones 2859* (GA). George Co.: along Hwy. 98, 0.5 mi. W. of Alabama-Mississippi state line, *Lelong 5200* (NCU). Tishomingo Co.: 6 mi. NE. of Iuka, *Ray 7522* (GH, MISSA, NCU). Wayne Co.: 5 mi. SE. of Shubata, *Ray 7004* (FSU, GH, MISSA, NCU). ARKANSAS. Drew Co.: near Monticello, *Demaree 13514* (NY). Hot Springs Co.: near Bismark, *Demaree 17415* (GH, NY). Ouachita Co.: near Stephens, *Demaree 16837* (NY). Pike Co.: near Langley, *Demaree 9517* (GH, NY). Pope Co.: Crow Mt., Galla Creek woods, *Tucker 7215* (NCU). Saline Co.: 2 mi. E. of Benton, *Demaree 35602* (NCU, VDB). Stone Co.: Ozark Natl. Forest, near Fiftysix, *Demaree 58226* (NCU, VDB). White Co.: about 0.5 mi. W. of Rosebud, *Redfearn 19239* (NCU). LOUISIANA. Ouachita Co.: Sec. 9, T. 17 N., R. 2 E., Tiger Branch off La. 838, *Thomas 11031* (VDB). Vernon Co.: about 2.5 mi. N. of Burr Ferry, *Thieret 27322* (DUKE, FSU). Washington Co.: 3 mi. NE. of Franklinton, *Correll 9198* (DUKE, GH). Webster Co.: 4 mi. W. of Minden, *Correll 10270* (DUKE, GH, NY). Winn Co.: 4 mi. W. of Winnfield, *Correll 10039* (DUKE, GH, NY). OKLAHOMA. LeFlore Co.: near Page, *Blakley 1427* (GH, US). Logan Co.: Jacks Creek camp, Strickland, *Demaree 15753* (NY). McCurtain Co.: 1.5 mi. SW. of Smithville, *Redfearn 19806* (NCU). Pushmataha Co.: along Little R., Honobia, *Waterfall 13023* (GH, US). TEXAS. Angelina Co.: N. edge of Boykin Springs, *Correll 16501* (GH). Bowie Co.: near Texarkana, *Heller 4178* (GH, NY). Newton Co.: E. of Newton, *Lundell 11881* (TEX). San Augustine Co.: San Augustine, *Palmer 10646* (A). Shelby Co.: 9.5 mi. SW. of Center, *McVaugh 8435* (GH, TEX). Tyler Co.: 6 mi. E. of Woodville, *Kral 29090* (ENCB, VDB).

Lyonia ligustrina is a rather isolated species, which is here placed in the monotypic section ARSENOCOCCUS, and is most closely related to the eastern Asian sect. PIERIDOPSIS. Quite variable in stature, pubescence, leaf size and shape, and inflorescence structure, it has been divided into numerous intergrading varieties (see, for example, Fernald, 1941), most of which are actually nothing more than extremes in the total pattern of variation. However, the populations of the Appalachian Mountains and northward can usually be readily differentiated from those of the southeastern Atlantic Coastal Plain from the Dismal Swamp (Virginia) southward, the Gulf Coastal Plain, and adjacent regions (MAPS 10, 11). The Appalachian Mountain and northern populations are here treated as *Lyonia ligustrina* var. *ligustrina*, while those of the southeastern Coastal Plain are considered as *L. ligustrina* var. *foliosiflora*. Variety *ligustrina* can be differentiated from var. *foliosiflora* by its inflorescences that lack leaflike bracts or have only a very few such bracts present, and by its often duller, less coriaceous leaves. In contrast, var. *foliosiflora* has conspicuously leafy inflorescences, and often more coriaceous and lustrous leaves.

Although these two varieties are morphologically distinguishable across wide geographic areas and are essentially geographically isolated, their ranges overlap slightly on the Coastal Plain of southeastern Virginia and the Carolinas, and in small areas of Georgia, northern Alabama, and adjacent parts of Tennessee. In these regions, especially the Carolinas, intermediate plants

can be found that are apparently perfectly fertile. Because these taxa differ in so few characters (and even these are rather difficult to quantify), and because they intergrade freely where they occur sympatrically, they are probably better treated as geographic varieties than as separate species (cf. Pursh, 1814; Elliott, 1817; Nuttall, 1818; and Small, 1903, 1913, 1933).

Michaux (1803) was the first to recognize infraspecific variation in *Lyonia ligustrina*. He recognized two primary varieties ("var. 1. *nudiflora*: racemes nudis" and "var. 2. *foliosiflora*: racemes foliosis"), each of them with two subvarieties. He gave the habitat of var. *nudiflora* as "frigidioribus, per *Etats-Unis*," and of var. *foliosiflora* as "in sylvis Carolinae inferioris" and "in stagnosis." Michaux was correct in giving the naked inflorescences as the most distinguishing character of var. *ligustrina* (= his var. *nudiflora*) and in recognizing the distinctness of the leafy-bracted plants of the Coastal Plain.

Populations of *Lyonia ligustrina* var. *ligustrina* in the southern Appalachians often show a tendency toward obovate or oblanceolate leaves with acuminate tips. The mountain populations are also often more pubescent. Plants with scattered large bracts in the inflorescences occur in the mountains of western North Carolina, the extreme northwestern portion of South Carolina, and northeastern Georgia.

Lyonia ligustrina var. *foliosiflora* is most variable on the Atlantic Coastal Plain, where two distinctive forms occur. Many plants have nearly glabrous or only sparsely pubescent, narrowly to widely elliptic, obovate or ovate leaves with acuminate apices. These plants tend to be laxly branched and to have large, very prominently leafy inflorescences and reddish twigs. Such plants are common on the Coastal Plain from southeastern Virginia (the Dismal Swamp), south to Florida, and west to Louisiana, eastern Texas, and southeastern Oklahoma. Very similar plants, but usually with larger leaves and less conspicuously leafy inflorescences, occur in the mountains of Arkansas. A few specimens representative of this form are: Virginia, *Fernald & Long* 4118 (GH), 14975 (GH); North Carolina, *Randolph* 637 (GH); South Carolina, *Little & Wood* 14305 (GH), *Godfrey & Tryon* 1405 (GH); Georgia, *Wood & Wilson* 9351 (GH); Florida, *Curtiss* 4718 (GH), *Harbison* 17 (GH), *Nash* 528 (GH); Mississippi, *Webster & Wilbur* 3423 (GH); Arkansas, *Demaree* s.n., 10-10-1960 (GH), *Palmer* 6972 (A), 29205 (A); Louisiana, *Correll* 9198 (GH); Oklahoma, *Palmer* 21595 (A), 22246 (A).

A second and less common form occurs chiefly in the Carolinas and Georgia and is especially distinct in South Carolina. This form consists of often rather small, rigidly ascending shrubs that have a moderate to dense covering of multicellular hairs and obovate to \pm elliptic leaves with mucronate to acute apices. These plants tend to have fewer floral bracts than do plants of the form described above. Extreme individuals have very coriaceous and densely pilose leaves with clearly revolute margins and prominently raised-reticulate veins on their abaxial surfaces. A few specimens characteristic of this form include: North Carolina, *Godfrey* 6948 (GH), 48177 (GH); South Carolina, *Godfrey & Tryon* 528 (GH), 906 (GH), 1106 (GH); Georgia, *Nuttall* s.n. (GH).

Although the "pubescent" and "glabrous" extremes of *Lyonia ligustrina*

var. *foliosiflora* appear to be quite different, the intergradation is so complete that, in practice, it is impossible to separate the two forms, especially when many collections from the Atlantic Coastal Plain are studied. The morphological extremes are isolated neither ecologically nor geographically and can be found (together with various intermediate plants) in the same localities. For these reasons, all of these plants are considered to be one rather variable taxon.

Michaux (1803) first pointed out the existence of the "pubescent" and "glabrous" extremes of *Lyonia ligustrina* var. *foliosiflora*. He described two unnamed subvarieties of his var. *foliosiflora*, "A. floribus glabellis" and "B. [floribus] subtomentosis." Both Rehder (1924) and Fernald (1941) considered these to be distinct varieties.

The axillary paniculate inflorescences of *Lyonia ligustrina* are produced near the end of the growth of the preceding year, often resulting in a prominent "pseudoterminal cluster." The number of inflorescences in this "cluster" varies from as high as 25 to as low as 1, and a single plant may have a widely varying number of inflorescences clustered at the ends of its branches.

Some confusion has existed concerning the plant to which the Linnaean name *Andromeda paniculata* (1753) refers. Aiton (1799), Willdenow (1799), and Michaux (1803) understood the description of Linnaeus to refer to *Lyonia ligustrina*. Pursh (1814) used *Andromeda paniculata*, and Nuttall (1818) used *Lyonia paniculata*, both in reference to *L. ligustrina* var. *ligustrina*. Others, such as K. Koch (1872) and A. Gray (1878), indicated that the *Andromeda paniculata* of Linnaeus was a different plant. Elliott (1817, p. 490) used *Andromeda ligustrina* for *Lyonia ligustrina* var. *ligustrina* and in the discussion under this taxon added:

To the accurate and extensive researches of Dr. Muhlenberg, American botanists are indebted for the real history of this plant. It appears to have been the original *Vaccinium ligustrinum* of Linnaeus; it certainly agrees with the Linnaean description of that plant as far as it extends. Modern botanists have viewed it as the *Andromeda paniculata* of Linnaeus, but whoever attends to the description of that plant, in the early additions of the Species Plantarum, will readily perceive that its great author must have had a very different one in view.

The views expressed by Elliott seem to be correct. The Linnaean description of *Andromeda paniculata* is quite ambiguous in that some characters seem to be describing a species of *Leucothoë*. The description seems to fit either *L. racemosa* (L.) Gray or *L. recurva* (Buckley) Gray with respect to three characters: "racemes secundis," "corollis sub-cylindricis," and "foliis . . . crenulatis." Yet Linnaeus's description does state that the racemes are naked and paniculate, characters that could be interpreted as referring to *Lyonia ligustrina*. Koch (1872) listed *Andromeda paniculata* L. as a synonym of *Leucothoë racemosa* (L.) A. Gray, which he called *Lyonia racemosa*. A specimen in the Linnaean Herbarium (sheet no. 563.14, microfiche photo seen), labeled *paniculata*, has the letter "K" near the base of the specimen, indicating that it was collected by P. Kalm. The sheet contains a fruiting specimen of *Lyonia ligustrina* var. *ligustrina* and a flowering specimen of

Leucothoë racemosa; this probably explains the confusing description given for *Andromeda paniculata* in the *Species Plantarum* (1753)! The name *Andromeda paniculata* is here lectotypified by the flowering element (i.e., *Leucothoë racemosa*). It should be noted that this same taxon was described by Linnaeus (1753) as *Andromeda racemosa*. The proper name of this species is thus *Leucothoë racemosa*.

Lyonia Nutt. sect. *MARIA* (DC.) C. E. Wood, Jour. Arnold Arb. **42**: 48. 1961.

Leucothoë D. Don sect. *Maria* DC. Prodr. **7**(2): 602. 1839. *Andromeda* L. sect. *Maria* (DC.) Gray, Man. Bot. No. U. S. 266. 1848. *Pieris* D. Don sect. *Maria* (DC.) Bentham & Hooker, Gen. Pl. **2**: 588. 1876. *Andromeda* subsect. *Maria* (DC.) Gray, Synopt. Fl. N. Am. **2**(1): 32. 1878. *Lyonia* Nutt. subg. *Maria* (DC.) Drude in Engler & Prantl, Nat. Pflanzenfam. IV. **1**: 44. 1889. *Neopieris* Britton & Brown, Illus. Fl. ed. **2**: 690. 1913. *Xolisma* Raf. sect. *Maria* (DC.) Rehder, Jour. Arnold Arb. **5**: 55. 1924. TYPE SPECIES: *Lyonia mariana* (L.) D. Don.

Desmothamnus Small, Shrubs Florida, 96. 1913. TYPE SPECIES: *Lyonia lucida* (Lam.) K. Koch.

Deciduous or evergreen shrubs, usually spreading vegetatively by horizontal underground rhizomes, the branches with homogeneous pith. Indumentum of unicellular hairs and multicellular, biseriate-stalked, mostly short-headed hairs. Buds with 2 to 6 (to 8) imbricate scales. Leaves entire, with unligified or only slightly lignified epidermis, lacking hypodermis. Flowers usually 5-merous, in fascicles; calyx lobes valvate in bud; corolla cylindrical, or cylindrical with swollen base; filaments with long, unicellular hairs near base or merely roughened, with pair of well-developed spurs below junction with anthers; placentae positioned centrally (to nearly basally) on columella. Capsules with pale, slightly to strongly thickened sutures that usually adhere to an adjacent valve in dehiscence; seeds oblong-ovoid to spindle shaped, ends often truncated.

DISTRIBUTION. Chiefly United States, Coastal Plain from Connecticut south to Florida, west to Oklahoma and eastern Texas; also in Cuba.

NUMBER OF SPECIES (taxa). 2 (2).

7. *Lyonia mariana* (L.) D. Don, Edinburgh New Philos. Jour. **17**: 159. 1834.

Andromeda mariana L. Sp. Pl. 393. 1753. *Andromeda pulchella* Salisb. Prodr. 289. 1796, *nomen superfluum*. *Leucothoë mariana* (L.) DC. Prodr. **7**: 602. 1839. *Pieris mariana* (L.) Bentham & Hooker, Gen. Pl. **2**: 588. 1876. *Neopieris mariana* (L.) Britton in Britton & Brown, Illus. Fl. ed. **2**: 691. 1913. *Xolisma mariana* (L.) Rehder, Jour. Arnold Arb. **5**: 51. 1924. Type: "habitat in Virginia," *Kalm s.n.* (lectotype, LINN sheet no. 563.5, microfiche photo seen).

Andromeda grandiflora Meerb. Pl. Select. Ic. Pictae, p. [8]. *t.* 25. 1798. TYPE: "Carol. merid," *J. Fraser s.n.* (lectotype, here designated, L!).

Andromeda mariana L. var. *ovata* Veillard in Duhamel, Traité Arbres Arbustes, ed. 2. 177. [1800-]1801-1819 (but this description probably

published ca. 1803). TYPE: (not seen).

Andromeda mariana L. var. *oblonga* Veillard in Duhamel, *Traité Arbres Arbustes*, ed. 2. 177. ca. 1803. TYPE: (not seen).

Andromeda mariana L. var. *latifolia* Pers. *Synopsis Pl.* 1: 481. 1805. TYPE: (not seen).

Andromeda mariana L. var. *ovalis* Sims, *Curtis's Bot. Mag.* 38: t. 1579. 1813. TYPE: (not seen).

Andromeda mariana L. var. *angustifolia* Pursh, *Fl. Am. Sept.* 1: 294. 1814. *Leucothoë mariana* (L.) DC. var. *angustifolia* (Pursh) DC. *Prodr.* 7: 602. 1839. TYPE: (not seen).

Xolisma mariana (L.) Rehder f. *vestita* Rehder, *Jour. Arnold Arb.* 5: 51. 1924. *Lyonia mariana* (L.) D. Don f. *vestita* (Rehder) Parks, *First Sci. Field Meet. Palmetto State Park, Texas*, 9. 1936. TYPE: United States, Texas, Hardin Co., sandy pine lands, Silsbee, 25 April 1916, *Palmer 9561* (holotype, A!).

Erect deciduous shrub to ca. 1.5 meters tall, with brownish to gray, shallowly and longitudinally furrowed bark, spreading vegetatively by horizontal underground rhizomes. Twigs terete to slightly ridged, slender, with few short-headed hairs, otherwise glabrous to moderately pubescent. Buds \pm conical to ovoid, 1–2.5 by 0.9–2 mm., with 2 to 6 (to 8) imbricate bud scales (depending upon age). Leaf blades narrowly to widely elliptic, ovate, or obovate, (2.5–)3–8(–10.5) by 1–4(–5) cm., \pm flat, chartaceous to slightly coriaceous, ca. 0.15–0.4 mm. thick; apex acute to rounded-mucronate or very slightly acuminate; base narrowly cuneate to rounded; margin entire, plane to slightly revolute; venation brochidodromous to eucamptodromous, with 3° veins reticulate to percurrent; adaxial surface with sparse short-headed hairs, often otherwise glabrescent, the midvein, especially proximal portion, with sparse to dense pubescence that sometimes extends to 2° (or even 3°) veins, the 3° and higher order veins slightly visible to obscure, the 2° veins not depressed; abaxial surface with sparse short-headed hairs, otherwise glabrous to densely pubescent on midvein and often also on 2°, 3°, or even higher order veins, the 3° and higher order veins slightly visible to obscure, the 2° veins slightly raised and visible, sinuous, irregular or smoothly arching, curving toward apex; petiole (1.5–)2–7.5 mm. long, with short-headed hairs, otherwise sparsely to densely pubescent adaxially or all around. Flower buds above vegetative buds; inflorescences fasciculate, to 15-flowered. Pedicels slender to moderately stout, 5–19 mm. long, with short-headed hairs, otherwise glabrous to densely pubescent; bracteoles opposite, basal, triangular to ovate, 0.8–2 mm. long, often persistent; bracts to ca. 4.5 mm. long, similar to bracteoles in shape, deciduous. Flowers usually 5-merous; calyx lobes elongate-triangular to linear, with acute to acuminate apices, often slightly swollen at base, 3–9.5 by 1–4 mm., valvate, both surfaces with scattered short-headed hairs, otherwise glabrous to densely pubescent, deciduous in fruit; corolla cylindrical, 7–14 by 4.5–9 mm., white or rarely pink, abaxially with very sparse short-headed hairs, often appearing glabrous; filaments almost completely covered with long-unicellular hairs, 4–7 mm. long, with 2 usually well-developed spurs below anther-filament junction, anthers 1.5–3 mm. long; ovary glabrous or occasionally very sparsely pubescent, placentae central to nearly basal. Capsule

ovoid with constricted and truncated apex, 4–6.5 by 3–6 mm., with very sparse short-headed hairs, otherwise glabrous or very sparsely pubescent, with pale, moderately to strongly thickened sutures that in dehiscence usually remain attached to an adjacent valve (but sometimes with age separate as unit from both valves); seeds 0.7–1.5 mm. long. (FIGURE 29; see also Meerburg (1798), Duhamel (1803), Sims (1813), Britton & Brown (1913), Harshberger (1916), Gleason (1952), Graves (1952), Grimm (1957), Vines (1960), Wood (1961), Radford, Ahles, & Bell (1968).)

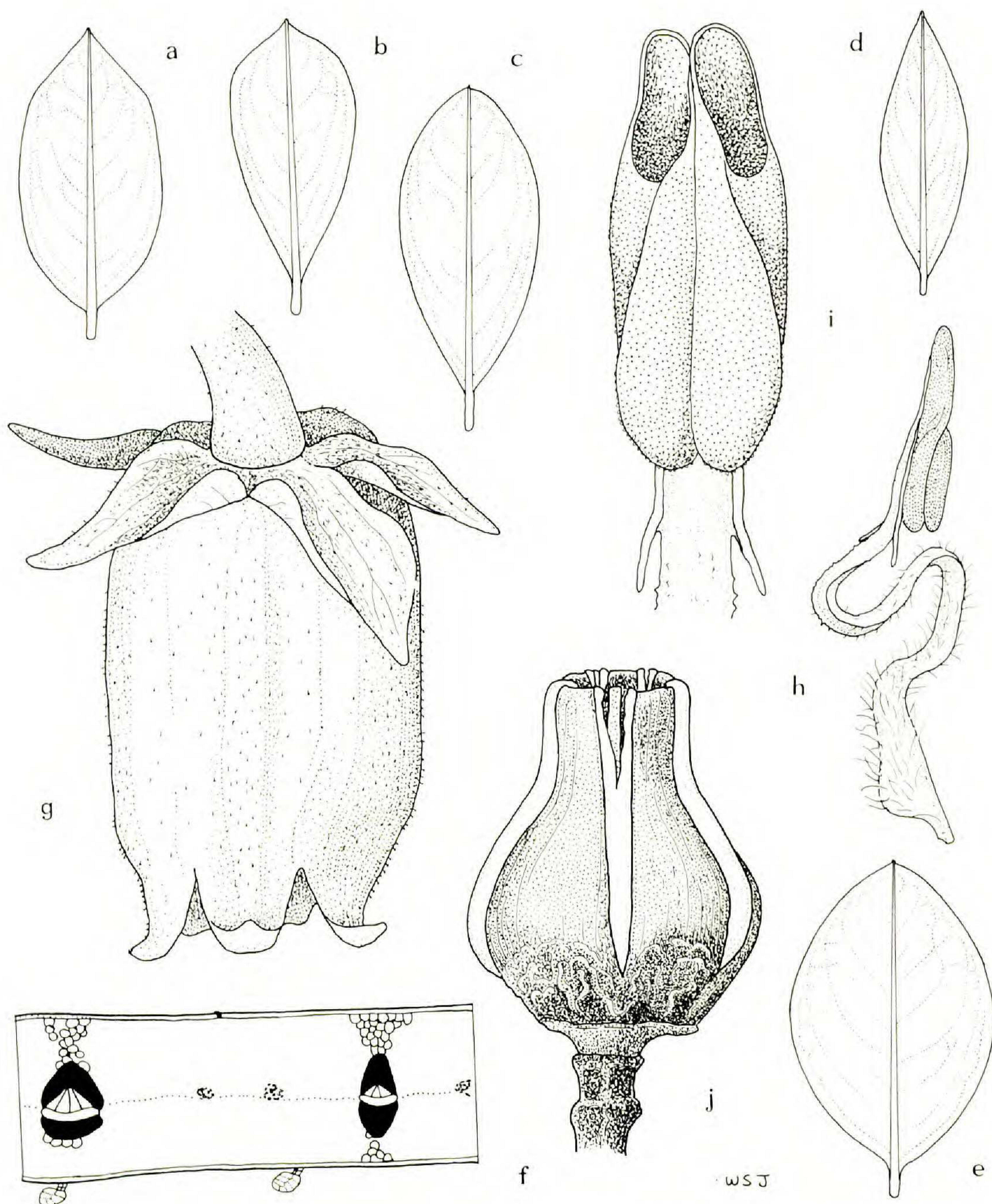
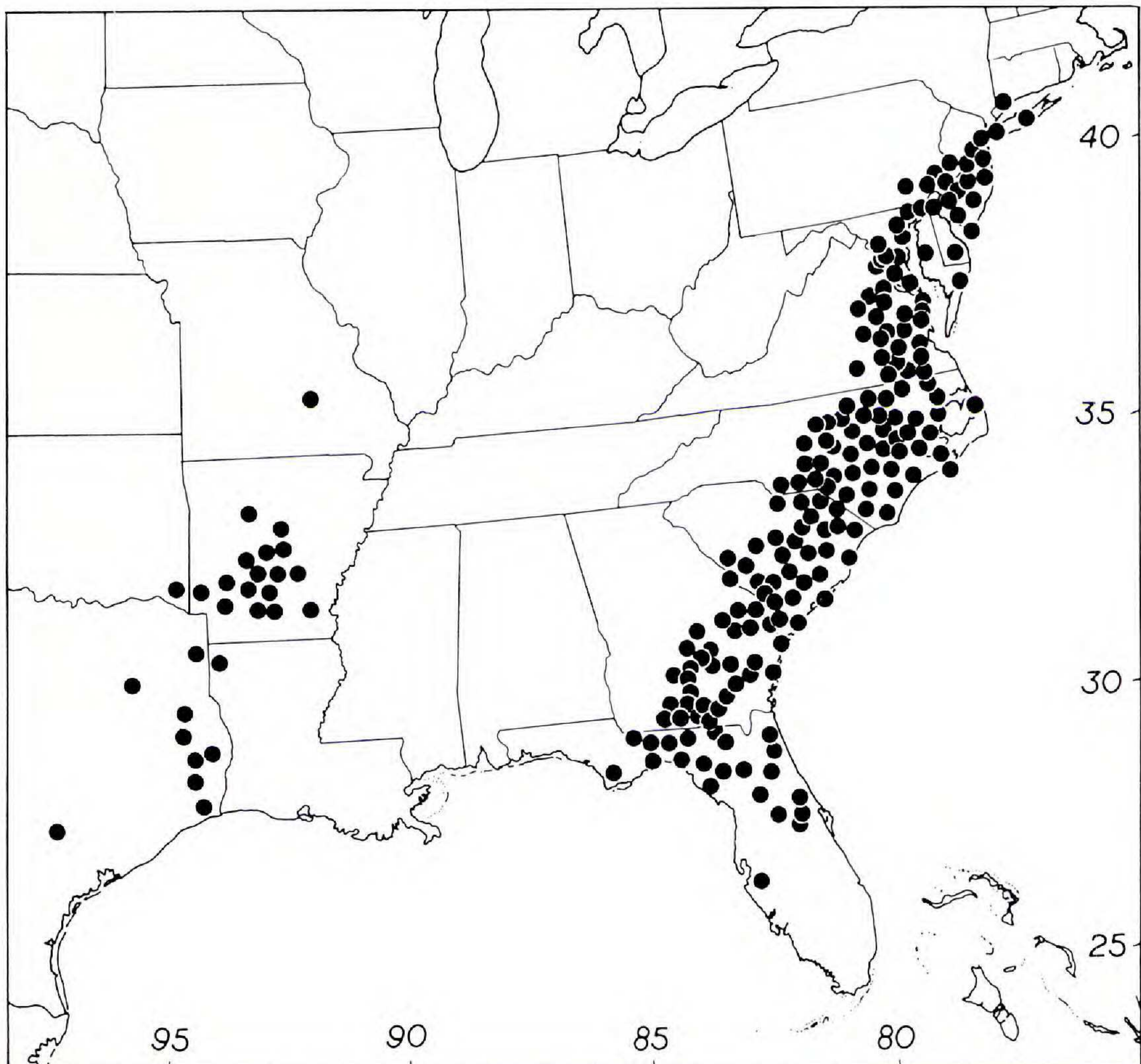


FIGURE 29. *Lyonia mariana*: a–e, leaves, $\times .5$; f, cross section of leaf blade, $\times 50$; g, flower, $\times 6$; h, stamen, $\times 12.5$; i, anther, adaxial surface, $\times 25$; j, capsule, $\times 6$.

DISTRIBUTION AND ECOLOGY. United States, chiefly Atlantic Coastal Plain from Connecticut and Long Island (New York) to Florida, with disjunct populations in eastern Texas, Louisiana, Arkansas, southeastern Oklahoma, and Missouri (MAP 12). Sunny habitats, forest margins, roadsides and railroad grades, shrub bogs, open *Pinus* and/or *Quercus* woods, thickets, old pastures, *Pinus rigida* barrens, *Pinus-Serenoa* flatwoods, grassy savannas, deciduous swamps (esp. of *Acer* or *Liquidambar*), pond margins, sheltered portions of coastal dunes. Flowering chiefly late April to early June.

COMMON NAMES. Stagger-bush, wicks.

REPRESENTATIVE SPECIMENS. **United States.** CONNECTICUT. Fairfield Co.: Stratford, *Coles s.n.*, July 1903 (CONN). NEW YORK. Nassau Co.: E. Williston, Long Island, *Churchill s.n.*, 28 Sept. 1899 (GH). Richmond Co.: N. shore, *Drushel* 6385 (US). Suffolk Co.: Ocean Beach, *Lighthipe s.n.*, Sept. 1913 (TEX). NEW JERSEY. Burlington Co.: Atsion, along Mullica R., *Churchill s.n.*, 15 June 1946 (MSC). Cape May Co.: Bennett Bog, 3.6 mi. N. of Cape May, *Crow* 109 (MSC). Cumberland Co.: 2 mi. E. of Milville, *Lems* 60.05.25.02 (MSC).



MAP 12. Distribution of *Lyonia mariana*.

Mercer Co.: N. of Maple Shade, *Long 53191* (GH). Monmouth Co.: near Asbury Park, *Van Sickle s.n.*, 12 July 1894 (US). PENNSYLVANIA. Chester Co.: Nottingham Barrens, *Pennell 1430* (US). Montgomery Co.: Willow Grove, *Wismer 69* (GH). DELAWARE. New Castle Co.: W. of Vandyke, *Tidestrom 11895* (GH). Sussex Co.: 0.8 mi. N. of Fenwick, *Judd 29* (MSC). MARYLAND. Anne Arundel Co.: Bodkin Creek, *Smith s.n.*, 1 June 1876 (US). Cecil Co.: Elks Neck, *Leonard 5993* (US). St. Marys Co.: 2 mi. W. of Clements, *Smith 5427* (US). Worcester Co.: near Snow Hill, *Gleason s.n.*, 6 June 1934 (DUKE). DISTRICT OF COLUMBIA: Swamp near Reform School, *McCarthy s.n.*, June 1885 (US). VIRGINIA. Caroline Co.: at Mattaponi R. off Co. Rd. 722, *James 13811* (NCU). Chesterfield Co.: E. of jct. of Co. Rd. 619 and U.S. 95, *James 5067* (NCU). Gloucester Co.: 3 mi. NW. of Gloucester Point, *Harvill 12440* (NCU). Louisa Co.: 1.5 mi. W. of jct. of Va. 22 and U.S. 522, *James 13832* (NCU). Lunenburg Co.: S. of Kenbridge, *James 3053* (NCU). Nansemond Co.: S. of South Quay, *Harvill 13828* (NCU). New Kent Co.: 1.4 mi. S. of jct. of Co. Rds. 637 and 1002, *Gillespie 624b* (NCU). NORTH CAROLINA. Beaufort Co.: 3 mi. S. of Chocowinity, *Radford 33395* (NCU). Brunswick Co.: 13 mi. NW. of Supply, *Wilbur 5533* (DUKE). Edgecombe Co.: 0.5 mi. S. of Speed, *Radford 36852* (NCU). Gates Co.: White Oak Pocosin, *Duke 780* (NCU). Onslow Co.: 1 mi. E. of Catherine Lake toward Chinquapin, *Wilbur 4081* (FSU). Orange Co.: 0.5 mi. E. of jct. of N.C. 87 and Route 1727, *Whigham 1992* (NCU). Randolph Co.: 4.4 mi. SE. of Liberty, *Bell 12037* (NCU). Sampson Co.: 2.8 mi. NNW. of Widway, *Ahles 24599* (NCU). Union Co.: 2 mi. WSW. of Marshville, *Ahles 27586* (NCU). SOUTH CAROLINA. Beaufort Co.: 1.1 mi. N. of Pritchardville, *Ahles 12374* (NCU). Berkeley Co.: 1.6 mi. S. of Wadboo Creek, *Bozeman 9145A* (NCU). Georgetown Co.: 5.5 mi. S. of Georgetown, *Godfrey & Tryon 199* (DUKE). Lancaster Co.: 0.4 mi. NNW. of Little Lynches Creek near U.S. 601, *Ahles 27435* (NCU). Lexington Co.: 3.5 mi. NE. of Gaston, *Radford 23379* (NCU). Marion Co.: S. of Britton Neck by Road 49, *Bell 7866* (NCU). GEORGIA. Appling Co.: 3 mi. SW. of Baxley, *Duncan 10925* (DUKE, MO, TEX). Effingham Co.: S. of Stillwell, *Bozeman 4108* (NCU). Laurens Co.: ca. 25 mi. S. of Dublin toward McRae, *Wilbur 3032* (FSU). Lowndes Co.: 10 mi. N. of Valdosta, *Faircloth 3739* (MO, NCU). Screven Co.: 3.5 mi. N. of Newington, *Kral 24024* (DUKE). Thomas Co.: N. of Thomasville, *Bozeman 4958* (NCU). Turner Co.: 3.7 mi. ENE. of Ashburn, *Faircloth 4353* (NCU). Ware Co.: near Suwannee Lake, *Harper 868* (NCU). FLORIDA. Duval Co.: near Jacksonville, *Curtiss 4717* (US). Lake Co.: Ocala Natl. Forest, SE. of Lake Dorr, *Ray 9835* (NCU). Manatee Co.: Palma Sola, *Tracy 6954* (MO, MSC). Marion Co.: Ocala Natl. Forest, *Mather M-142* (GA). Taylor Co.: 4 mi. N. of Perry, *McDaniel & Godfrey 4312* (FSU, NCU). Volusia Co.: 1.5 mi. E. of Astor bridge, *Kral 6566* (FSU). Wakulla Co.: near Wakulla, *Moldenke 1121a* (DUKE). MISSOURI. Dent Co.: 2 mi. S. of Lake Spring, T. 35 W., R. 7 W., sects. 15, 16, *Kucera s.n.*, 11 May 1953 (GA). ARKANSAS. Clark Co.: 2 mi. S. of Hot Springs–Clark Co. line, *Tucker 6889* (NCU). Drew Co.: near Monticello, *Demaree 14978* (MO, WIS). Faulkner Co.: Cove Creek, *Buchholz 979* (TEX, WIS). Grant Co.: near Poyen, *Demaree 11050* (GA). Pope Co.: Crow Mt., *Tucker 7214* (NCU). Saline Co.: near Bauxite, *Demaree 53814* (VDB). Sevier Co.: near Horatio, *Brinkley 169* (TEX). LOUISIANA. Caddo Co.: 4.5 mi. NW. of Vivian, *Thieret 32265* (DUKE, FSU). OKLAHOMA. McCurtain Co.: 2.7 mi. N. of Tom, *Waterfall 13002* (US). TEXAS. Gonzales Co.: Palmetto State Park, *Reis 106* (DUKE). Hardin Co.: Silsbee, *Correll 29392* (ENCB, FSU, GH, NCU, TEX, US). Henderson Co.: 11 mi. SW. of Athens, Spring Lake, *Correll 29612* (FSU, GH). Jasper Co.: 23 mi. NW. of

Jasper, *Cory* 22229 (A). Marion Co.: near Jefferson, *Biltmore Herb.* 25g (US). Tyler Co.: 2 mi. S. of Warren, *Correll* 35830 (ENCB, FSU, GH, NCU).

Lyonia mariana is a very distinctive deciduous species that can be recognized immediately by its entire-margined leaves covered with multicellular, short-headed hairs; its flowers borne in fascicles along the upper portions of leafless branches of the previous year; its large, white, more or less cylindrical corollas; its elongated, deciduous calyx lobes; and its peculiar, urn-shaped capsules. It is most closely related to *L. lucida*.

The western populations (see MAP 12) tend to be much more pubescent than those of the Atlantic Coastal Plain, and the most densely pubescent plants of the western region have been described as *Lyonia mariana* f. *vestita* (Rehder, 1924). The branchlets, calyx, and leaves of this form have a moderate to dense covering of long, soft, unicellular hairs; however, there are western plants that are only sparsely pubescent, and some eastern plants that are densely covered with unicellular hairs on the major veins of the leaves. In all other characters the plants of these two regions are identical.

The extensive network of underground rhizomes present in *Lyonia mariana* adapts it well to surviving fires. Many vigorous shoots have been observed growing around charred older branches where the plants had evidently been burned the previous year (pers. obs.).

Lyonia mariana has not been collected in Connecticut since 1903 and is probably extinct there, since the area in which it grew has become increasingly urbanized. Thus, Long Island is probably the present northern limit of its range. The species is also rare in Missouri (occurring only in Dent Co.) and Oklahoma (only in McCurtain Co.).

8. *Lyonia lucida* (Lam.) K. Koch, *Dendr.* 2: 118. 1872.

Andromeda lucida Lam. *Encycl.* 157. 1783. *Desmothamnus lucidus* (Lam.) Small, *N. Am. Fl.* 29(1): 64. 1914. *Pieris lucida* (Lam.) Rehder, *Mitt. Deutsch Dendrol. Ges.* 24: 266. 1915, non *Pieris lucida* Lévl. *Bull. Soc. Bot. France* 6: 207. 1906. *Xolisma lucida* (Lam.) Rehder, *Jour. Arnold Arb.* 5: 50. 1924. LECTOTYPE: P-LA (IDC 6207. 404: III. 2!).

Andromeda nitida Bartram ex Marsh. *Arbust. Am.* 8. 1785. *Pieris nitida* (Bartram ex Marsh.) Bentham & Hooker, *Gen. Pl.* 2: 588. 1876. *Lyonia nitida* (Bartram ex Marsh.) Fern. *Rhodora* 10: 53. 1908. *Neopieris nitida* (Bartram ex Marsh.) Britton in Britton & Brown, *Illus. Fl. ed. 2.* 2: 690. 1913. *Desmothamnus nitidus* Small, *Shrubs Florida*, 96. 1913. TYPE: "grows naturally in Carolina and Florida" (BM?, not seen).

Andromeda coriacea Aiton, *Hortus Kew.* 2: 79. 1789. *Andromeda myrtifolia* Salisb. *Prodr.* 290. 1796, *nomen superfluum*. *Leucothoë coriacea* (Aiton) DC. *Prodr.* 7: 602. 1839. TYPE: "Nat. of North Am., Mr. John Cree" (BM?, not seen).

Andromeda marginata Veillard in Duhamel, *Traité Arbres Arbustes*, ed. 2 (Nouv. Duhamel). 188. [1800-]1801-1819 (this description probably published in 1803). *Lyonia marginata* (Veillard) D. Don, *Edinburgh New Philos. Jour.* 17: 159. 1834. *Leucothoë marginata* (Veillard) Spach, *Hist. Veg.* 9: 482. 1840. TYPE: "La Caroline et la Floride" (not seen).

Andromeda nitida Bartram ex Marsh. var. *rhombofolia* Wood, *Class Book*, ed. 1861. 488. 1861. TYPE: (not seen).

Andromeda lacustris C. Wright in Sauvage, Anal. Acad. Ci. Habana **6**: 250. 1870. TYPE: Cuba, en "tembladeras" de lagunas cerca de Pinar del Río dentro de los pinales, C. Wright 3664 (holotype, us!; isotypes, GH!, NY (3 sheets)!, P!).

Andromeda coriacea Aiton var. *rubra* Lodd. Bot. Cab. **7**: 672. 1822. *Lyonia marginata* (Veillard) D. Don var. *rubra* (Lodd.) Loudon, Arb. Frut. Brit. **2**: 1110. fig. 901. 1838. *Pieris nitida* (Bartram ex Marsh.) Benth. & Hooker var. *rubra* (Lodd.) Rehder in Bailey, Cycl. Am. Hort. **5**: 2622. 1916. *Xolisma lucida* (Lam.) Rehder var. *rubra* (Lodd.) Rehder, Man. Cult. Trees Shrubs, 712. 1927. *Lyonia lucida* (Lam.) K. Koch f. *rubra* (Lodd.) Rehder, Jour. Arnold Arb. **20**: 425. 1935. TYPE: "Carolina and Georgia, growing in sandy forests" (not seen).

Small to moderate-sized evergreen shrub to 2.5(-5) meters tall, with brownish to gray, shallowly and longitudinally furrowed bark, usually spreading vegetatively by horizontal underground rhizomes. Twigs usually sharply 3-angled, slender, erect to arching, with few short-headed hairs, otherwise glabrous to moderately pubescent. Buds ovoid, 1-3 by 0.7-1.5 mm., with 2 to 6 imbricate bud scales (depending upon age). Leaf blades narrowly to widely elliptic, obovate, or slightly ovate, 1-8.5(-10.5) by 0.5-4.5(-5.5) cm., sometimes quite reduced in size toward branch apices, \pm flat, quite coriaceous, ca. 0.2-0.45 mm. thick; apex acuminate to acute or rarely rounded; base attenuate or cuneate to rounded; margin entire, usually revolute; venation modified brochidodromous, 3° veins \pm reticulate; adaxial surface sparsely covered with short-headed hairs, otherwise \pm glabrescent, sometimes sparsely pubescent on proximal portion of midvein, 2° and 3° veins usually obscure to slightly raised and visible; abaxial surface with sparse short-headed hairs, otherwise glabrous, the 3° and higher order veins usually obscure, the 2° veins slightly raised and visible, extending straight (or by slightly arching path) toward margin where they join to form intramarginal vein; petiole 1-8 mm. long, with short-headed hairs, otherwise glabrous or pubescent adaxially; vascular bundle unifacial or occasionally slightly bifacial. Flower buds above vegetative buds; inflorescences fasciculate, to 10- (to 15-)flowered. Pedicels slender to stout, 2.5-13 mm. long, with short-headed hairs, otherwise glabrous to densely pubescent; bracteoles opposite, basal, triangular to ovate, 1-2.5 by ca. 1.5 mm., often persistent; bracts to ca. 4 mm. long, similar to bracteoles in shape. Flowers 5-merous; calyx lobes persistent, elongate-triangular, usually with acute apices, 2-7.5 by 1-2 mm., usually swollen at base; the adaxial side very sparsely to moderately pubescent, the abaxial side with scattered short-headed hairs, otherwise glabrous to moderately pubescent; corolla usually cylindrical with swollen base (often appearing merely cylindrical after drying), 5-9 by 2.5-5 mm., pink, less commonly white or red, abaxially with very sparse short-headed hairs, often appearing glabrous; filaments roughened, 3-5 mm. long, with 2 usually well developed spurs below anther-filament junction, anthers 0.8-1.5 mm. long; ovary glabrous or with few short-headed hairs, placentae central to nearly basal. Capsule ovoid to ovoid-globose, occasionally slightly urn-shaped, 3-5 by 3-5 mm., glabrous or with very few short-headed hairs, with pale, slightly to strongly thickened

sutures that usually remain attached to an adjacent valve in dehiscence; seeds 0.7–1.3 mm. long. (FIGURE 30; see also Duhamel (1803), Curtis (1808), Loddiges (1822), Britton & Brown (1913), Small (1927, 1933), Brown (1945), Gleason (1952), Vines (1960), Wood (1961), Radford, Ahles, & Bell (1968).)

DISTRIBUTION. United States, chiefly Coastal Plain from southeastern Virginia (the Dismal Swamp) to Florida, west to Louisiana, also in Cuba (Pinar del

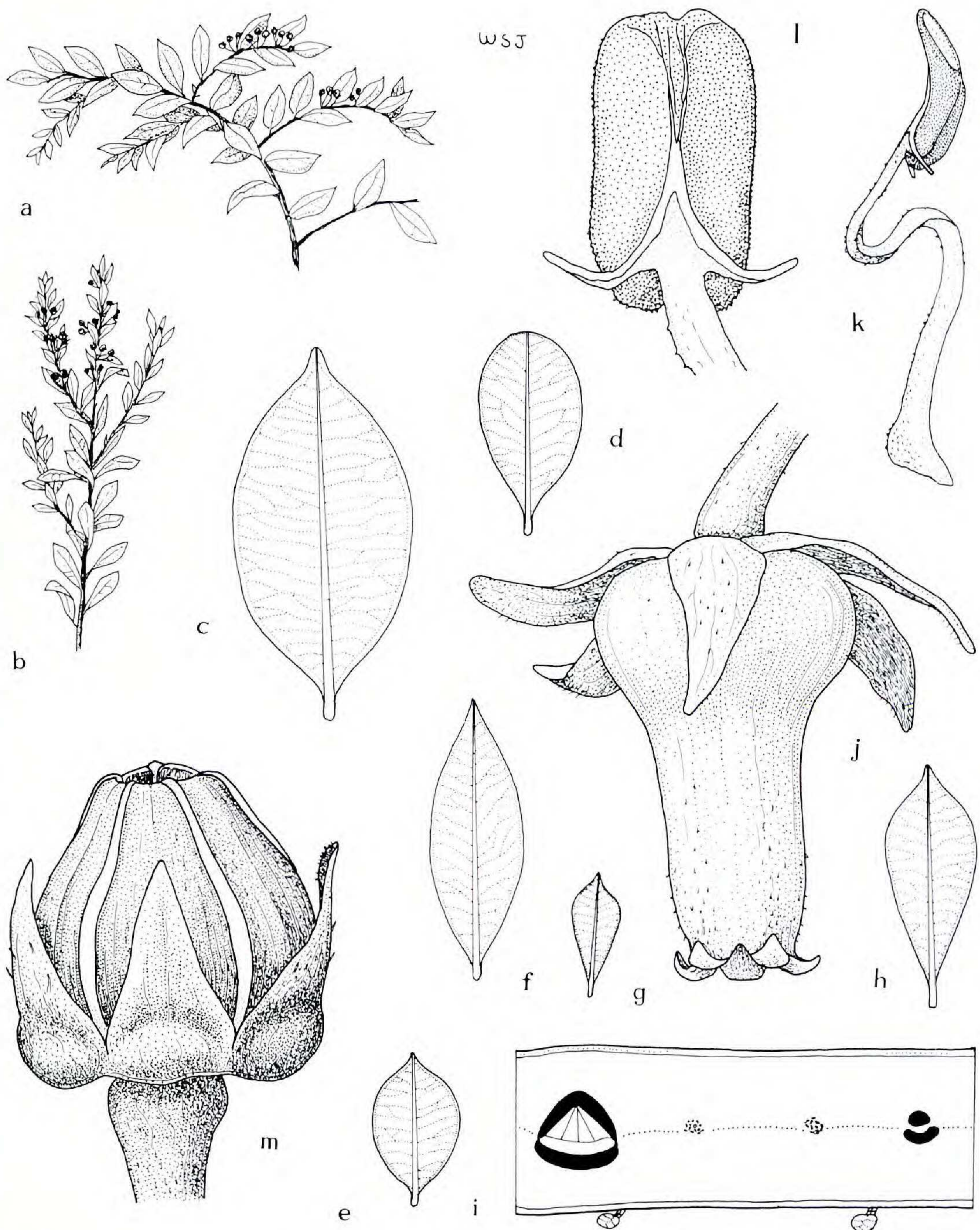
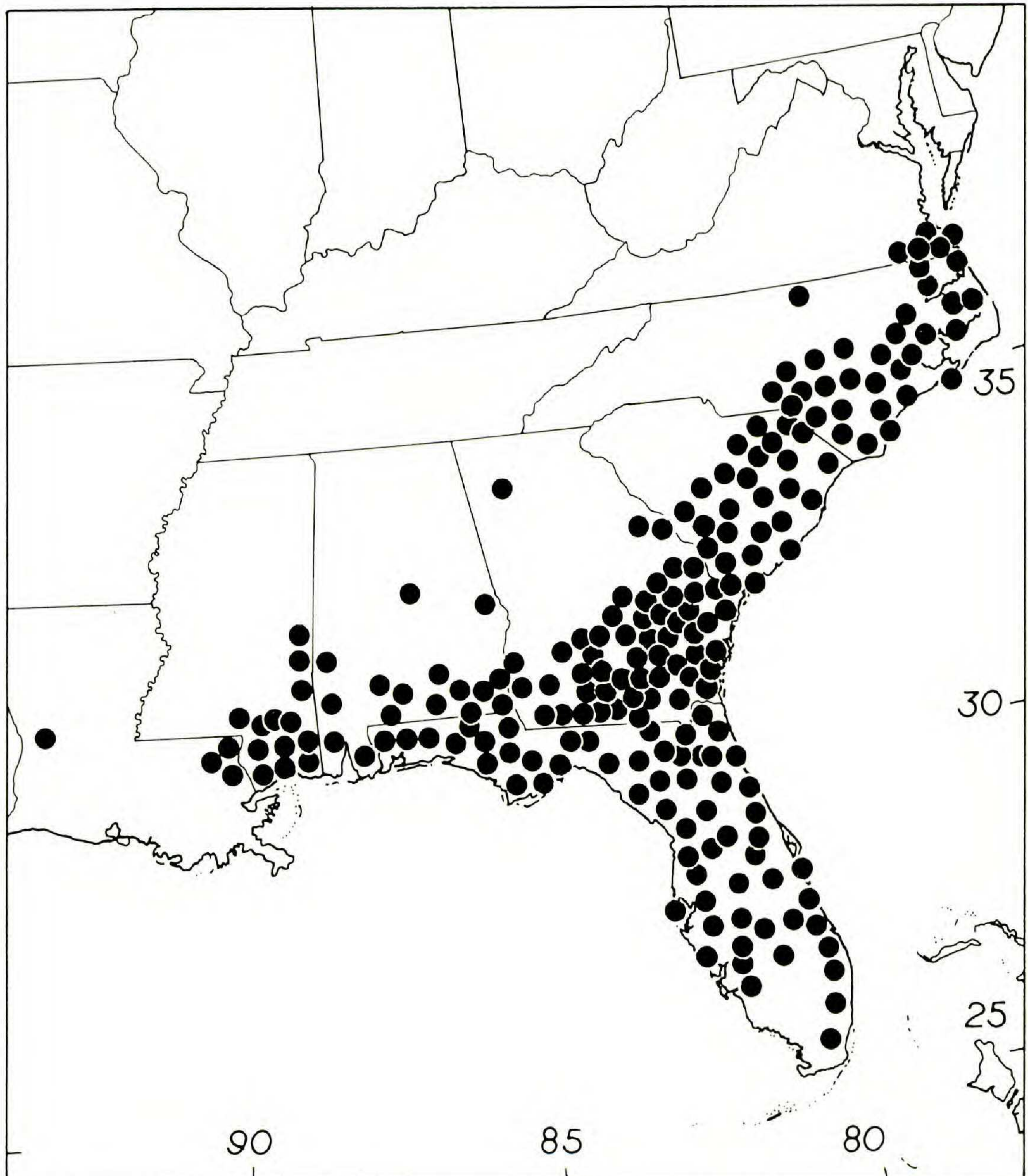


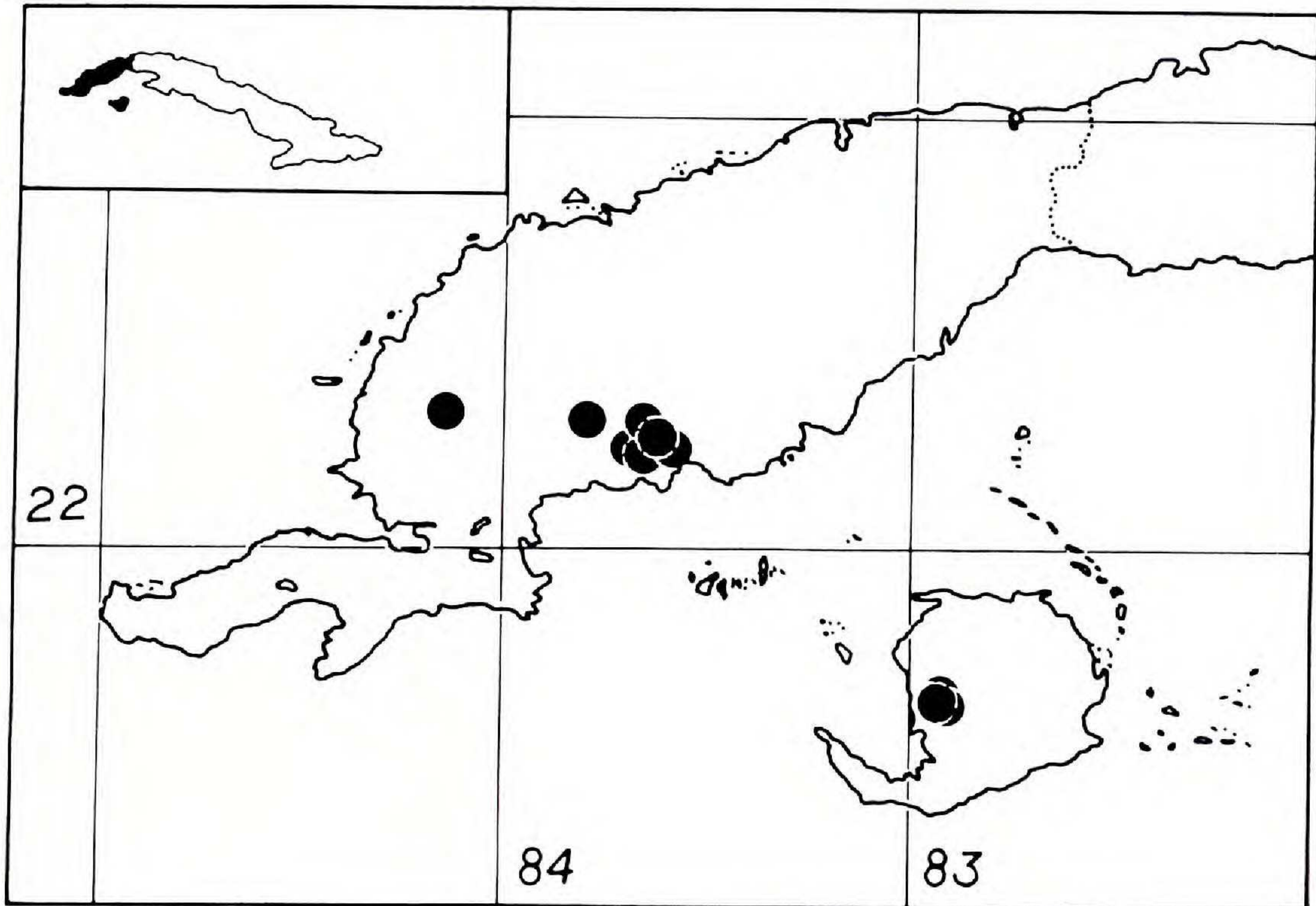
FIGURE 30. *Lyonia lucida*: a, habit in moist, shaded site; b, habit in dry, sunny site; c–h, leaves, $\times .5$; i, cross section of leaf blade, $\times 50$; j, flower, $\times 6$; k, stamen, $\times 12.5$; l, anther, $\times 25$; m, capsule, $\times 6$.



MAP 13. Distribution of *Lyonia lucida* in the United States.

Río prov., Isle of Pines) (MAPS 13, 14). Some interesting disjunct populations around several small ponds in Bartow Co., Georgia (see Greear, 1967).

ECOLOGY. In southeastern U.S., in *Taxodium* swamps, especially around margins, or at base of cypress trees (pers. obs.; see also Coker (1912, esp. pl. 12, photograph of dead *Taxodium* with dense collar of *Lyonia* and other shrubs surrounding it at water level) and Lemon (1945)). Very common in many broadleaved swamps; often dominant in moist *Pinus* savannas, shrub-bogs (pocosins), *Pinus-Serenoa* flatwoods, sand scrub and thickets, moist *Pinus* and/or *Quercus* forests, and swamp or pond margins. In Cuba, chiefly in white-sand *Pinus* savannas and near pond margins (Jennings, 1917; Marie-



MAP 14. Distribution of *Lyonia lucida* in Cuba.

Victorin & León, 1944; Seifriz, 1943; Alain, 1946b; Smith, 1954). Flowering mainly late March to early May in southeastern U.S.; chiefly November and December in Cuba.

COMMON NAMES. Fetter-bush, stagger-bush, hurrah-bush (U.S.); clavellina (Cuba).

REPRESENTATIVE SPECIMENS. **United States.** VIRGINIA. Isle of Wight Co.: S. of Zuni, *Harvill 12043* (NCU). Nansemond Co.: 1 mi. SE. of Blackwater R. on Va. 189, then 2.5 mi. S., *Ahles 58125* (NCU). Southampton Co.: 7 mi. S. of Franklin, *Harvill 13950* (NCU). Virginia Beach: N. of Blackwater R., *Fernald & Long 4116* (GH). NORTH CAROLINA. Beaufort Co.: 3 mi. S. of Chocowinity, *Radford 33404* (NCU). Brunswick Co.: 12 mi. NW. of Supply, *Wilbur 10739* (DUKE). Currituck Co.: Grandy, on U.S. 158, *Ahles 40151* (NCU). Johnston Co.: 2 mi. S. of Parker's Hill, *Radford 27832* (NCU). Onslow Co.: W. of Jacksonville, *Ahles 24076* (NCU). Richmond Co.: Solomon Creek, *J. L. H. s.n.*, 13 Nov. 1917 (NCU). Sampson Co.: 1 mi. NE. of Midway, *Ahles 24608* (NCU). SOUTH CAROLINA. Aiken Co.: 3 mi. NW. of Beech Is., *Radford 9251* (NCU). Berkeley Co.: 5.3 mi. SSE. of jct. of U.S. 176 and S.C. 27, *Ahles 22383* (NCU). Chesterfield Co.: 7.7 mi. N. of McBee, *Radford 13432* (NCU). Horry Co.: Myrtle Beach, *Christenberry s.n.*, 14 July 1938 (NCU). Jasper Co.: 5.5 WNW. of Tillman, *Leonard 1267* (FSU). Richland Co.: along S.C. 12, 1.9 mi. SW. of Kershaw Co. line, *Duke 1614* (NCU). GEORGIA. Bartow Co.: 4.5 mi. SE. of Adairsville, near Quicksand Pond, *Greear 6315* (NCU). Brooks Co.: 3 mi. E. of Quitman, *Bozeman 4899* (NCU). Camden Co.: S. end of Cumberland Is., *Judd 1723* (A, FLAS). Clay Co.: Ft. Gaines, *Wiggington s.n.*,

27 Dec. 1952 (GA). Jeff Davis Co.: 7 mi. SW. of Hazelhurst, *Wilbur 3198* (GH). Lee Co.: near Smithville, *Oosting 78* (DUKE). Liberty Co.: 11 mi. E. of Taylor Creek, *Duncan 2237* (GA). Tattnall Co.: 1.9 mi. NW. of Reidsville, *Ahles 54258A* (NCU). Ware Co.: 10 mi. SW. of Waycross, *Murphy 2410* (NCU). FLORIDA. Bay Co.: St. Andrew State Park, *Wooten 209* (FSU). Duval Co.: 1 mi. S. of Mayport, *Godfrey 61201* (FSU). Dade Co.: W. of Fulford, *Moldenke 454* (DUKE). Lee Co.: Alva, *Hitchcock 191* (US). Leon Co.: Silver Lake Recr. Area, *Lems s.n.*, 8, 10, 11 July 1959 (MSC). Levy Co.: about 5 mi. NE. of Cedar Key, *Godfrey 52824* (FSU, NCU). Polk Co.: near Lake Wales, *Demaree 49452* (FSU, NCU). Union Co.: near Olustec Creek and Road 28, *West & Arnold*, 22 May 1942 (FLAS). Volusia Co.: Tomoka Game Preserve along tributary to Little Tomoka R., *Prichard 968* (FSU). Walton Co.: about 4 mi. W. of Paxton, *Godfrey 61257a* (FSU). ALABAMA. Baldwin Co.: 2 mi. SW. of Theodore, *Iltis et al. 21590* (ENCB, NCU, WIS). Chilton Co.: 6.3 mi. NE. of Clanton, *Clark 17636* (NCU). Covington Co.: 6 mi. NW. of Red Level, *Clark 14422* (NCU). Henry Co.: near Abbeville, *Harbison 4101* (NCU). Lee Co.: Auburn, *Earle & Baker s.n.*, 8 July 1897 (NCU). Mobile Co.: 1 mi. N. of Satuma, *Iltis et al. 21410* (NCU, WIS). Washington Co.: along Bassett's Creek, near U.S. 43 bridge, *Clark 8739* (NCU). MISSISSIPPI. Clarke Co.: 7 mi. SE. of Quitman, *Ray 6986* (MISSA). Forrest Co.: 2 mi. NW. of Eatonville, *Ray 7761* (NCU). Hancock Co.: near Bay St. Louis, *Demaree 32974* (DUKE, MISSA, TEX). Harrison Co.: near Mississippi City, *Demaree 35541* (FSU, NCU). Marion Co.: about 2 mi. S. of Sandy Hook, *Ray 7911* (MISSA). LOUISIANA. St. Tammany Co.: about 3 mi. SE. of Abita Springs, *Thieret 26964* (DUKE, FSU). Tangipahoa Co.: 13 mi. E. of Hammond, *Rose-Innes & Warnock 723* (TEX). Vernon Co.: Kisatchie Natl. Forest, *Cooley & Brass 4026* (NCU). **Cuba.** PINAR DEL RÍO: dry Arroyo Mántua, Damují, *Ekman 11036* (NY); Laguna Santa Maria, S. of Río Feo, vicinity of Pinar del Río City, *Ekman 17282* (K, US); Pinar del Río City, at km. 11 on rd. to Coloma, *Ekman 18253* (K, NY, US); near Laguna Redonda, 11 km. S. of Pinar del Río, *Bro. León et al. 17775* (GH); vicinity of Sumidero, *Shafer & Bro. León 13632* (F, MO, NY, US). ISLA DE PINOS: LOS INDIOS, *Bro. Alain & Killip 2216* (GH, US).

Lyonia lucida is a very distinctive species characterized by coriaceous, persistent, entire-margined leaves with an intramarginal vein and scattered, multicellular, more or less short-headed hairs; fasciculate inflorescences; elongated calyx lobes; usually pink, more or less cylindrical corollas with a swollen base; and roughened filaments with two usually well-developed spurs just below the anther-filament junction. It is also unusual in that the vascular tissue of the leaf midrib and petiole is unifacial or nearly so.

Lyonia lucida is most closely related to *L. mariana*. Although *L. lucida* lacks the strikingly urn-shaped capsule (see FIGURES 29, 30) of *L. mariana*, it often does have the slightly constricted capsule apex; both species tend to have more or less central to nearly basal placentae bearing many ovules. The two species can often be seen growing in close proximity, although *L. lucida* is usually found in wetter situations. Hybrids between these species have apparently never been found.

Lyonia lucida is quite variable in leaf size and shape and in habit. In sunny, dry environments it tends to be a dwarf shrub with rigidly ascending branches bearing very small and narrow leaves, while in damp, shaded localities

it is often quite a large shrub with beautifully arching branches and large, more or less elliptic leaves. When a narrow-leaved plant collected in the dry pine-palmetto scrub of southeastern Georgia was transplanted to the moist environment of a greenhouse, it developed large, elliptic leaves, thus indicating that this difference is mainly environmentally controlled.

The Cuban populations often have slightly longer and more densely pubescent calyx lobes than do plants on the Coastal Plain of the southeastern United States, but in all other respects plants of the two regions are identical.

To be concluded